University of Alberta

RESPONSE OF HIGH ARCTIC PLANTS, *EQUISETUM ARVENSE* AND *DUPONTIA FISHERI*, TO EXPERIMENTAL WARMING AND BARNACLE GOOSE HERBIVORY IN SVALBARD, NORWAY

by

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ABSTRACT

Arctic ecosystems are warming rapidly. Recent work has explored the impacts of this warming on tundra vegetation. Changes in tundra productivity and biodiversity will impact the global carbon budget, and trophic interactions. I conducted one of the first studies to explicitly acknowledge the significant effects of herbivores on vegetation productivity, composition, and morphology in a climate change context. I experimentally explored the effects of warming and herbivory by barnacle geese on *Equisetum arvense*, and *Dupontia fisheri*, in a wet tundra valley, in Svalbard, Norway. Both species responded to warming when stressed by herbivory. *E. arvense* had a blended, intermediate response to the combined factors, whereas warming delayed the induction of a short-leaved, herbivory-tolerant morphology in *D. fisheri* by one year. These results show that trophic interactions must be considered when predicting the effects of climate change on Arctic vegetation.

Acknowledgements

When I first saw the advertisement for a Masters position in Svalbard, I had just finished a nice bowl of mutton soup and a good cup of Ulaan Baatar salty tea before checking my email. I had been under the mistaken impression that I already was at the edge of the Earth. Thank you to David Hik for forwarding that advertisement on to me, and to Elisabeth Cooper and Ingibörg Jónsdóttir for accepting my application, and subsequently providing the opportunity to rectify my opinion. I am grateful to all three supervisors for their expertise and enthusiasm throughout the course of this project.

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CHAPTER 1

GENERAL INTRODUCTION

The Arctic flora

The terrestrial Arctic biome is highly heterogeneous, complex, and characterized by extreme fluctuations in environmental conditions (Jónsdóttir 2005; Pohl and Marsh 2006). Plant growing seasons range from 1 to 3 months, multiple months of sunlight are followed by multiple months of darkness, soil organic content can range from zero to 30%, and mean July temperatures can be as low as 1°C (Maxwell 1992; Jónsdóttir 2005). In addition, nutrient concentrations, especially nitrogen, frequently limit primary productivity (Bazely and Jefferies 1985; Shevtsova *et al.* 2005). Despite these adverse growing conditions, plants grow, compete with and facilitate each other, and provide the resource base for a range of vertebrate and invertebrate herbivores (Dormann and Brooker 2002; Dormann *et al.* 2004; Larter and Nagy 2004; Olofsson *et al.* 2004; Olofsson 2006). Multiple levels of interactions among and between invertebrates and microbes control decomposition and mineralization of carbon and nitrogen, the limiting resources for plants and upper trophic levels (Bardgett *et al.* 2002; Hodkinson and Coulson 2004; Jónsdóttir 2005).

A unique characteristic of the Arctic biome is the high number of species common to all continents and landmasses (i.e. Panarctic Flora Project, e.g. Siegismund and Philipp 1999; Brysting *et al.* 2004). The Arctic flora originated in the late Pliocene (Matthews and Ovenden 1990) and has expanded and contracted

with subsequent ice ages where species have remained in refugia during glacial events (Abbott and Brochmann 2003). While Arctic plants are robust to considerable environmental variation, they are sensitive to rapid change. Most Arctic plants are characterized by perennial, slow-growing life-cycles and predominantly asexual reproduction (Brochmann *et al.* 2004). These traits can reduce their abilities to respond to rapid change.

Climate change

Arrhenius (1897) first proposed the idea that anthropogenic sources of carbon dioxide can increase the insulating capacity of the Earth's atmosphere in the late nineteenth century. Given little credence at the time, there is now substantial evidence indicating that carbon dioxide and other greenhouse gasses from anthropogenic sources are causing this contemporary warming (IPCC 2001). The concentrations of carbon dioxide (380 ppm) and methane (1880 ppb) in the atmosphere are currently in excess of the ranges observed in the past 420 000 years (carbon dioxide 180-280 ppm; methane 400-700 ppb) (Petit *et al.* 1999; World Data Centre for Greenhouse Gases 2006). The combustion of fossil fuels rapidly releases carbon sequestered from the atmosphere by primary producers over millions of years into our current atmosphere and is the primary source of anthropogenically released carbon dioxide (Vitousek *et al.* 1997; IPCC 2001). In addition, changes in land use release substantial amounts of carbon dioxide as well as methane, nitrous oxide, and other greenhouse gases into the atmosphere (Dale 1997; Vitousek *et al.* 1997). Synthetic greenhouse gases are new to the

atmosphere, some have extremely long atmospheric lives (eg. F_4, C_2F_6, and SF_6 exist in the atmosphere >1000 years), and some have extremely high contributions to radiative forcing on a per molecule basis (SF_5C_3 19 000 times more potent than CO_2) (IPCC 2001; Nielsen *et al* 2002; Forster and Joshi 2005). Significant reductions in atmospheric carbon dioxide concentration, through sequestration in primary producers, is a slow process acting over tens of thousands of years. It is unlikely humanity will cease inputting greenhouse gases into the atmosphere and consequently these levels will rise further. Over geological time, there is a strong correlation between atmospheric carbon dioxide and methane concentrations and temperature (Petit *et al.* 1999; IPCC 2001). Thus further warming of the global climate appears inevitable.

There are many uncertainties surrounding this warming and its effects, and both negative and positive feedbacks have been suggested (e.g. aerosols, changes in thermohaline circulation, reductions of polar ice cover and resultant changes in albedo (Charlson 1992; IPCC 2001; Higgins and Schneider 2005; Hock 2005)). The response of vegetation and soils to warming and higher carbon dioxide levels is one issue being debated. Higher concentrations of carbon dioxide can increase primary productivity and sequester carbon more rapidly (DeLucia *et al.* 1999; Smith *et al.* 2000). However, rates of decomposition and soil respiration may increase in response to warmer temperatures causing the release of carbon in the form of either methane or carbon dioxide, sequestered in permafrost, and wetland soils (Davidson *et al.* 2000; Knorr *et al.* 2005; Davidson and Janssens 2006, but see Giardina *et al.* 2000a; Giardina *et al.* 2000b).

To better understand these interactions many studies have been conducted in the Arctic. Polar regions are warming more rapidly than temperate areas (ACIA 2005). Changes occurring in the Arctic can provide insight and be indicative of the responses other biomes may experience in later years. The island archipelago of Svalbard, in the European Arctic is predicted to warm by 0.3 - 1.1 °C per decade over the next 50 years (Benestad *et al.* 2002). This warming will have significant effects on the ecosystems and organisms inhabiting them (ACIA 2005).

Plant-herbivore interactions

Herbivory is a biologically prominent component of most ecosystems on Earth (Milchunas and Lauenroth 1993). The relationship between plants and herbivorous animals is ancient, and their co-evolution has resulted in an arsenal of chemical and structural weapons and defences to attack and counter each other (e.g. Bezemer *et al.* 2003; Kimball and Nolte 2005; Kapari *et al.* 2006). In response to herbivory, plants can defend (e.g. secondary metabolites, structural defences such as spines), tolerate (e.g. basal meristems found in the grasses), hide (reduce apparency) or die (Atsatt and O'Dowd 1976; Chew and Courtney 1991; Rosenthal and Kotanen 1994). Herbivory pressure, competition intensity with neighbours, and the environmental conditions dictate which strategies will be successful and consequently which species will subsist (Herms and Mattson 1992). Thus herbivores can have strong effects on species composition, standing

crop, nutrient cycling and can have significant effects on soil properties (e.g. compaction, nutrient concentrations, soil invertebrate species).

The resources available to vegetation limit productivity, and herbivores are limited by vegetation in the absence of predators, however when predators are abundant they can limit herbivores (Fretwell 1977; Oksanen *et al.* 1981). Under certain conditions herbivory can have positive effects on plants, increasing productivity (McNaughton 1983), or even fitness (Paige 1992), although these cases are the minority and herbivory typically functions through negative influences on plants (Belsky *et al.* 1993).

Invertebrates likely consume more plants than vertebrate herbivores on a global scale (Danelle and Bergstrom 2002), however the diversity of invertebrate herbivores decreases with increasing latitude. In a dry heath area of Svalbard, where a detailed food web was mapped, invertebrate herbivores of vascular plants were represented by one species of sawfly, one species of aphid, and nine species of collembola (although these collembola were also found on non-vascular plants and in the detrital food web) (Hodkinson and Coulson 2004). Vertebrate herbivores by comparison can remove upwards of 50% of net above ground primary productivity (Jefferies *et al.* 1992). Although the abundance and importance of invertebrate herbivores may increase with warming, the emphasis on past herbivory research has been placed on vertebrate herbivores because of their dominant effects.

Geese

Migratory herbivores are particularly important as they provide a link between biomes that are spatially separated. Through this migratory connectivity, events occurring in other ecosystems, political states and even continents can have significant impacts on ecosystems thousands of kilometres away (Webster *et al.* 2002). All goose species breeding in the Arctic are migratory herbivores, connecting mid-latitude temperate biomes to high latitude Arctic biomes. In the past century major changes in land use and advances in agriculture in the United States and Southern Canada have had particularly significant effects on tundra ecosystems in the Canadian Arctic through migratory geese (Robertson and Slack 1995; Jefferies *et al.* 2004; Abraham *et al.* 2005). Larger areas dedicated to agriculture and the advent of fertilizer use have increased crop production. Remnants from harvesting provide an exploitable resource for migratory geese in their wintering grounds (Alisauskas *et al.* 1988; Jefferies *et al.* 2000; Jefferies *et al.* 2004). Increases in lesser snow geese (*Chen caerulescens caerulescens*), greater snow geese (*Chen caerulescens altlantica*), and Canada geese (*Branta canadensis*) have been well documented (Ankney 1996; Jefferies *et al.* 2000; Jefferies and Rockwell 2002a). The natural predators of geese did not increase proportionately in the summering grounds in parts of Northern Canada, likely because winter resources restrict predator population growth (Jefferies *et al.* 2004). In response to the dramatic increases in goose populations a spring hunt was introduced in 1999 in both Canada and the United States.

The effects of snow geese on vegetation have been studied extensively in a sub-arctic salt-marshes at La Perouse Bay, Manitoba, Canada. Large snow goose populations have intense effects on the vegetation, and can cause two ecologically stable states on the salt-marsh vegetation depending on herbivory pressure. Grazed swards of highly herbivore-tolerant graminoids can increase aboveground production (overcompensation) in response to high levels of herbivory (Hik and Jefferies 1990; Hik *et al.* 1991). Overgrazing and grubbing of below-ground plant parts causes the soil to become hypersaline and the destruction of vascular plant growing conditions (Srivastava and Jefferies 1996). The first stable state results in a positive feedback where geese graze above-ground portions of plants and rapidly recycle the nitrogen back to the highly herbivory-tolerant graminoid species through their faeces and promote nitrogen fixing blue-green algae (Hik and Jefferies 1990; Hik *et al.* 1991; Walker *et al.* 2003). In this situation geese promote growth of highly herbivory-tolerant graminoids such as *Puccinellia phryganodes* and *Carex subspathacea,* while delaying colonization of less tolerant and less digestible graminoids such as *Calamagrostis deschampsioides* and *Festuca rubra* (Hik *et al.* 1992; Zellmer *et al.* 1993) The second stable state results from grubbing and foraging of geese on the below-ground plant parts. This causes a loss of rhizomes, organic matter, the seed bank, and nitrogen as cyanobacterial mats on sediment dry out and blow away in the summer causing an increase in soil salinity (Srivastava and Jefferies 1996; Jefferies and Rockwell 2002b; Walker *et al.* 2003). Evaporation further exacerbates the salinity and vegetation recovery may take decades (Handa and Jefferies 2000; Handa *et al.*

2002; Jefferies and Rockwell 2002b). Consumption of below-ground plant parts occurs when snowmelt is late and geese arrive prior to vegetation green-up.

The situation described above occurs in a Low Arctic salt-marsh where productivity is relatively high and graminoid species that are highly tolerant to herbivory grow from sediment. Another well-studied system is on Bylot Island, a site in the High Arctic, where graminoids grow from a thick moss layer. At this site greater snow geese preferentially graze *Eriophorum scheuchzeri*, and to a lesser extent *Dupontia fisheri* when goose densities are high (Gauthier *et al.* 1995). A series of experiments have shown that neither species increases productivity as a result of grazing or addition of goose faeces (Beaulieu *et al.* 1996). Compensation for lost tissue is through below-ground resources (Beaulieu *et al.* 1996). Gauthier *et al.* 1995 suggest this is because moss competes with the graminoids for nitrogen from goose faeces and blue-green algae do not colonize the bare sediment.

Many barnacle and pink-footed goose populations in Europe are also increasing in response to land use changes in their wintering areas (Madsen *et al.* 1999; Fox *et al.* 2005). Additionally, hunting has been restricted on geese in their wintering grounds and new bird refuges have been established further increasing their numbers. In Svalbard, these two goose species utilize different resources in the pre-breeding season. Barnacle geese forage on only aboveground material whereas pink-footed geese select belowground material (Fox and Bergersen 2005).

FRAGILE

In response to concerns over increasing goose numbers in Europe, the EU funded project FRAGILE (Fragility of Arctic Goose habitat: Impacts of Land use, conservation, and Elevated temperature) was formed. The aim of FRAGILE is to provide policy makers and wildlife managers in the European Union with an understanding of the factors influencing population numbers of barnacle geese and pink footed geese, and to provide scientific predictions of the impacts of geese in their current and projected future habitats. Specifically, FRAGILE examines changes in land use, conservation strategies, and the potential impacts of climate change in habitats used by geese, particularly in the European Arctic, through modelling and field experiments. This thesis was conducted within the framework of FRAGILE, specifically within the group studying the effects of climate change and herbivory on the tundra ecosystems. Further details on FRAGILE can be found at: http://www.fragile-eu.net/.

Study site

This study was conducted in Adventdalen valley on the island of Spitsbergen, Svalbard, Norway from 2004 to 2005 (78°63'N, 15°22'W, elevation 25-50 m above sea level). The primary site was on wet tundra where moisture was maintained over the summer by snow and ice melt off nearby mountains and glaciers. The dominant vascular plant species were *Equisetum arvense (L.)* and *Dupontia fisheri* (*R. Br.)* and the dominant moss species was *Calliergon*

richardsonii (Mitt). This vegetation was typical of High Arctic wetland vegetation (CAVM Team 2003).

Study species

Equisetum arvense is a common plant that is frequently considered a weed in temperate regions. Its distribution extends from temperate regions to the high Arctic and from damp forests to sandy areas (Cody 1996). It is one of the 15-20 extant species in the phylum Sphenopsid (Gifford and Foster 1989). It has a rhizomatous growth form, and can reproduce clonally, through fragmentation and sexually through spores (Sakamaki and Ino 2002; Cloutier and Watson 1985). Few studies have examined how this species responds to either warming or herbivory.

Dupontia fisheri is a perennial graminoid. It is exclusive to high latitude, wet tundra conditions and is found in the European, Russian and North American Arctic (Brysting *et al.* 2004). It likely originated from an intergeneric hybridization between *Arctophila fulva* and another species that has not yet been identified (Brysting *et al.* 2004). It reproduces predominantly through clonal growth although seed set is possible.

Barnacle geese (*Branta leucopsis*) are a European 'black' goose species similar to the North American Canada goose. They winter in Scotland, Ireland, England, and the Netherlands and breed in Greenland, Svalbard, Novaya Zemlya and along the shores of the Baltic Sea. Unlike pink-footed geese and snow geese,

barnacle geese are predominantly grazers and do not grub belowground plant parts (Fox and Bergersen, 2005).

Study objectives

In this study, I examined how individual plant ramets respond to warming when they are also under herbivory stress. I used a controlled factorial experiment, using open-topped chambers (hexagonal ITEX design; Marion *et al.* 1997) to warm the tundra and captive barnacle geese to graze plots for specified amounts of time. I examined the growth, productivity, plant morphology and below-ground reserves of target plant species. In contrast to the majority of herbivory and climate change studies conducted in dry tundra areas, I sampled in wet areas.

In chapter 2, I focus on selectivity of geese, and the responses of below-ground rhizomes, and above-ground growth patterns to warming and herbivory. *Equisetum arvense* is an important species in Arctic environments because its long rhizomes transport nutrients from deep in the soil to the surface (Marsh *et al.* 2000). It is also a preferred forage species for many animals, yet little is known of its responses to herbivory. Additionally, because of its unique growth form, the typical plant functional groupings partitioned by climate change scientists do not apply and thus little is known of its response to warming. I examined both responses individually and their combined effects.

In chapter 3, I focus on the responses in above-ground productivity, below-ground reserves, and above-ground morphology of *Dupontia fisheri* to experimental treatments. I explore the tradeoffs associated with plant

morphologies associated with herbivory compared to morphologies that optimize production under warmer temperatures.

In chapter 4, I review my major findings and main conclusions, discuss their implications and identify areas of future research.

Figure 1-1 Map of the Earth indicating Svalbard. Modified from: Collins 1999.

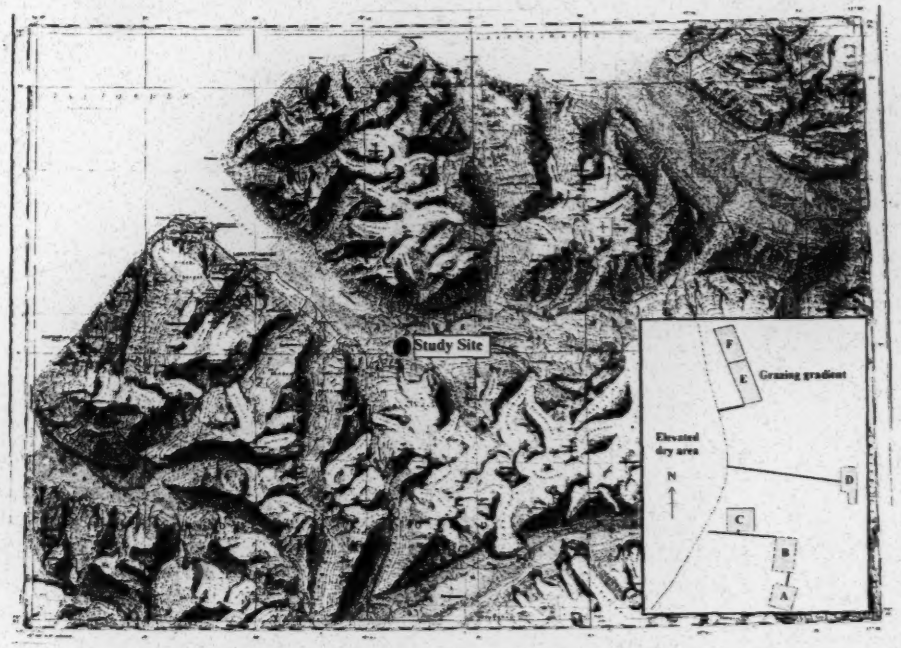

Figure 1-2 Map of Adventdalen indicating the FRAGILE study site. Modified from: Norsk Polarinstitutt 2003. Inset: Layout of study site. Letters indicate blocks.

Figure 1-3 Work on an ungrazed Open-Topped-Chamber (OTC). Ladders were suspended between boardwalks to avoid trampling effects. A heavily grazed, ambient plot in foreground and Adventdalen valley in background. Photo credit: Adriana Koziak.

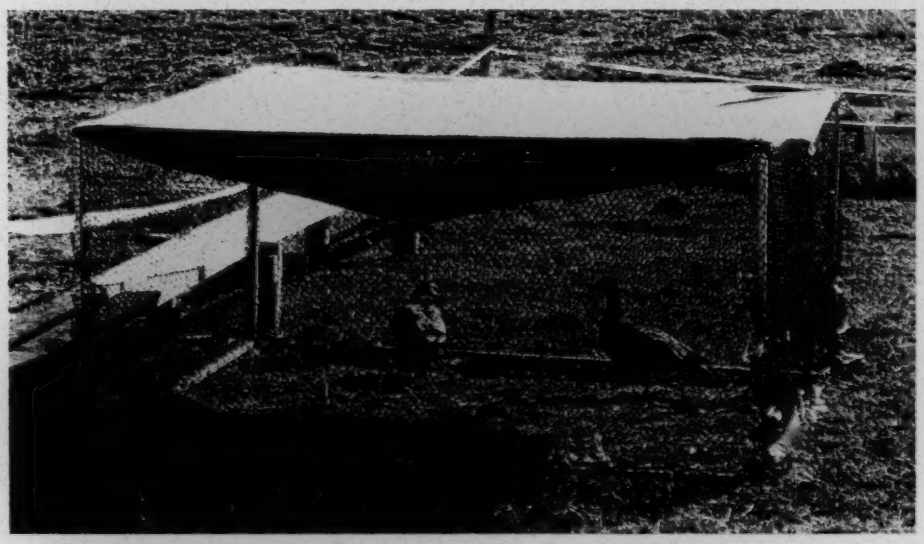

Figure 1-4 Grazing event. Two barnacle geese were placed on a plot for either 1 or 5 hrs during a grazing event. Photo credit: Terra Birkigt.

Figure 1-5 Study site showing three of the five experimental blocks. Each block contained the six treatment combinations. Adventdalen valley in background. Photo credit: Terra Birkigt.

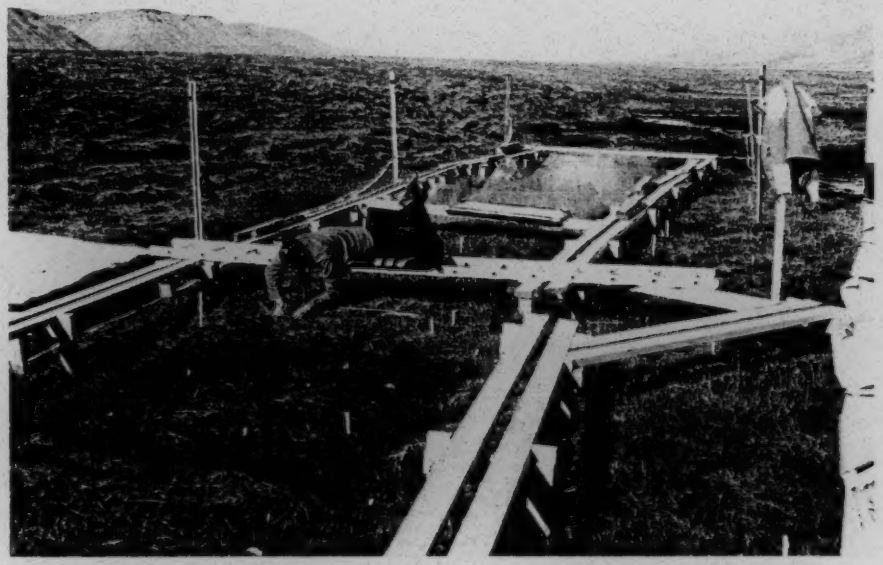

Figure 1-6 Work on an ungrazed plot. OTCs in background, Ambient plots in foreground. Photo credit: Adriana Koziak.

Literature cited

Abbott RJ, Brochmann C (2003) History and evolution of the Arctic flora: in the footsteps of Eric Hulten. *Molecular Ecology*, **12,** 299-313.

Abraham KF, Jefferies RL, Alisauskas RT (2005) The dynamics of landscape change and snow geese in mid-continent North America. *Global Change Biology*, **11**, 841-855.

Abraham KF, Jefferies RL, Rockwell RF (2005) Goose-induced changes in vegetation and land cover between 1976 and 1997 in an Arctic coastal marsh. *Arctic Antarctic and Alpine Research*, **37,** 269-275.

ACIA (2005) Arctic Climate Impact Assessment. Cambridge University Press, Cambridge.

Alisauskas RT, Ankney CD, Klaas EE (1988) Winter diets and nutrition of midcontinental lesser snow geese. *Journal of Wildlife Management*, **52**, 403-414.

Ankney CD (1996) An embarrassment of riches: Too many geese. *Journal of Wildlife Management*, **60**, 217-223.

Arrhenius S (1896) On the influence of carbonic acid in the air upon the temperature of the ground. *Philosophical Magazine*, **41**, 237-276.

Atsatt PR, Odowd DJ (1976) Plant defense guilds. *Science*, **193**, 24-29.

Bardgett RD, Streeter TC, Cole L, Hartley IR (2002) Linkages between soil biota, nitrogen availability, and plant nitrogen uptake in a mountain ecosystem in the Scottish highlands. *Applied Soil Ecology*, **19**, 121-134.

Bazely DR, Jefferies RL (1985) Goose feces - a source of nitrogen for plant-growth in a grazed salt-marsh. *Journal of Applied Ecology*, **22**, 693-703.

Beaulieu JG, Gauthier G, Rochefort L (1996) The growth response of graminoid plants to goose grazing in a High Arctic environment. *Journal of Ecology*, **84**, 905-914.

Belsky AJ, Carson WP, Jensen CL, Fox GA (1993) Overcompensation by plants - herbivore optimization or red herring. *Evolutionary Ecology*, **7**, 109-121.

Benestad RE, Forland EJ, Hanssen-Bauer I (2002) Empirically downscaled temperature scenarios for Svalbard. *Atmospheric Science Letters*, **3**, 71-93.

Bezemer TM, Wagenaar R, Van Dam NM, Wackers FL (2003) Interactions between above- and belowground insect herbivores as mediated by the plant defense system. *Oikos*, **101**, 555-562.

Brochmann C, Brysting AK, Alsos IG, Borgen L, Grundt HH, Scheen AC, Elven R (2004) Polyploidy in Arctic plants. *Biological Journal of the Linnean Society*, **82**, 521-536.

Brysting AK, Fay MF, Leitch IJ, Aiken SG (2004) One or more species in the Arctic grass genus *Dupontia*? - a contribution to the Panarctic Flora Project. *Taxon*, **53**, 365-382.

CAVM Team (2003) Circumpolar Arctic vegetation map. Scale 1:7 500 000. Conservation of Arctic Flora and Fauna (CAFF) Map No. 1. U.S. Fish and Wildlife Service, Anchorage, Alaska.

Charlson RJ, Schwartz SE, Hales JM, Cess RD, Coakley JA, Hansen JE, Hofmann DJ (1992) Climate forcing by anthropogenic aerosols. *Science*, **255**, 423-430.

Chew FS, Courtney SP (1991) Plant apparency and evolutionary escape from insect herbivory. *American Naturalist*, **138**, 729-750.

Cloutier D, Watson AK (1985) Growth and regeneration of field horsetail (*Equisetum Arvense*) *Weed Science*, **33**, 358-365.

Cody WJ (1996) *Flora of the Yukon Territory*. NRC Research Press, Ottawa, 643 pp.

Collins (1999) *Collins Mini Atlas of the World.* Harper Collins Publishers. Haddington, Scotland 253 pp.

Dale VH (1997) The relationship between land-use change and climate change. *Ecological Applications,* **7**, 753-769.

Danelle K, Bergstrom R (2002) Mammalian herbivory in terrestrial environments. In: *Plant-Animal Interactions An Evolutionary Approach* (eds Herrera CM, Pellmyr O), pp. 107-131. Blackwell Science, Cornwall.

Davidson EA, Janssens IA (2006) Temperature sensitivity of soil carbon decomposition and feedbacks to climate change. *Nature*, **440**, 165-173.

Davidson EA, Trumbore SE, Amundson R (2000) Biogeochemistry – soil warming and organic carbon content. *Nature*, **408**, 789-790.

DeLucia EH, Thomas RB, Ward JK (1999) Critical assessment of the response of forest ecosystems to elevated atmospheric carbon dioxide - Preface. *Tree Physiology*, **19**, Preface.

Dormann CF, Brooker RW (2002) Facilitation and competition in the High Arctic: the importance of the experimental approach. *Acta Oecologica-International Journal of Ecology*, **23**, 297-301.

Dormann CF, Van der Wal R, Woodin SJ (2004) Neighbour identity modifies effects of elevated temperature on plant performance in the High Arctic. *Global Change Biology*, **10**, 1587-1598.

Forster PMD, Joshi M (2005) The role of halocarbons in the climate change of the troposphere and stratosphere. *Climatic Change*, **71**, 249-266.

Fox AD, Bergersen L (2005) Lack of competition between barnacle geese *Branta leucopsis* and pink-footed geese *Anser brachyrhynchus* during the pre-breeding period in Svalbard. *Journal of Avian Biology*, **36**, 173-178.

Fox AD, Madsen J, Boyd H, Kuijken E, Norriss DW, Tombre IM, Stroud DA (2005) Effects of agricultural change on abundance, fitness components and distribution of two Arctic nesting goose populations. *Global Change Biology*, **11**, 881-893.

Fretwell SD (1977) Regulation of plant communities by food-chains exploiting them. *Perspectives in Biology and Medicine*, **20**, 169-185.

Gauthier G, Hughes RJ, Reed A, Beaulieu J, Rochefort L (1995) Effect of grazing by greater snow geese on the production of graminoids at an Arctic site (Bylot Island, NWT, Canada). *Journal of Ecology*, **83**, 653-664.

Giardina CP, Ryan MG (2000a) Evidence that decomposition rates of organic carbon in mineral soil do not vary with temperature. *Nature*, **404**, 858-861.

Giardina CP, Ryan MG (2000b) Biogeochemistry - soil warming and organic carbon content - Reply. *Nature*, **408**, 790-790.

Gifford EM, Foster AS (1989) Sphenophyta. In: *Morphology and Evolution of Vascular Plants* 3rd edition. 1959 Freeman. New York, 626 pp.

Handa IT, Harmsen R, Jefferies RL (2002) Patterns of vegetation change and the recovery potential of degraded areas in a coastal marsh system of the Hudson Bay lowlands. *Journal of Ecology*, **90**, 86-99.

Handa IT, Jefferies RL (2000) Assisted revegetation trials in degraded salt-marshes. *Journal of Applied Ecology*, **36**, 944-985.

Herms DA, WJ Mattson (1992) The dilemma of plants - to grow or defend. *Quarterly Review of Biology*, **67**, 283-335.

Higgins PAT, Schneider SH (2005) Long-term potential ecosystem responses to greenhouse gas-induced thermohaline circulation collapse. *Global Change Biology*, **11**, 699-709.

Hik DS, Jefferies RL (1990) Increases in the net aboveground primary production of a salt-marsh forage grass - a test of the predictions of the herbivore-optimization model. *Journal of Ecology*, **78**, 180-195.

Hik DS, Sadul HA, Jefferies RL (1991) Effects of the timing of multiple grazings by geese on net aboveground primary production of swards of *Puccinellia-phryganodes*. *Journal of Ecology*, **79**, 715-730.

Hik DS, Jefferies RL, Sinclair ARE (1992) Foraging by geese, isostatic uplift and asymmetry in the development of salt-marsh plant communities. *Journal of Ecology*, **80**, 395-406.

Hock R (2005) Glacier melt: a review of processes and their modeling. *Progress in Physical Geography*, **29**, 362-391.

Hodkinson ID, Coulson SJ (2004) Are high Arctic terrestrial food chains really that simple? The Bear Island food web revisited. *Oikos*, **106**, 427-431.

IPCC (2001) IPCC Third Assessment Report – Climate Change 2001.

Jefferies RL (2000) Allochthonous inputs: integrating population changes and food-web dynamics. *Trends in Ecology and Evolution*, **15**, 19-22.

Jefferies RL, Rockwell RF (2002a) An overabundance of lesser snow geese and an apparent trophic cascade. *Integrative and Comparative Biology*, **42**, 1250-1250.

Jefferies RL, Rockwell RF (2002b) Foraging geese, vegetation loss and soil degradation in an Arctic salt marsh. *Applied Vegetation Science*, **5**, 7-16.

Jefferies RL, Rockwell RF, Abraham KE (2004) Agricultural food subsidies, migratory connectivity and large-scale disturbance in Arctic coastal systems: A case study. *Integrative and Comparative Biology*, **44**, 130-139.

Jefferies RL, Svobboda J, Henry G, Raillard M, Ruess R (1992) Tundra grazing systems and climatic change. In: *Arctic Physiological Processes in a Changing Climate.* (eds Chapin T, Jeffries D, Reynolds J, Shaver G, Svoboda J) pp. 391-412. Academic Press, San Diego.

Jónsdóttir IS (2005) Terrestrial ecosystems on Svalbard: heterogeneity, complexity and fragility from an Arctic island perspective. *Biology and Environment: Proceedings of the Royal Irish Academy*, **105B**, 155-165.

Kapari LE, Haukioja M, Rantala J, Ruuhola Top (2006) Defoliating insect immune defense interacts with induced plant defense during a population outbreak. *Ecology*, **87**, 291-296.

Kimball BA, Nolte DL (2005) Herbivore experience with plant defense compounds influences acquisition of new flavor aversions. *Applied Animal Behaviour Science*, **91**, 17-34.

Knorr W, Prentice IC, House JI, Holland EA (2005) Long-term sensitivity of soil carbon turnover to warming. *Nature*, **433**, 298-301.

Larter NC, Nagy JA (2004) Seasonal changes in the composition of the diets of Peary caribou and muskoxen on Banks Island. *Polar Research*, **23**, 131-140.

Madsen J, Cracknell G, Fox AD, eds (1999) *Goose populations of the Western Palearctic. A Review of Status and Distribution.* Wetlands International Publication 48. Wetlands International/National Environmental Research Institute, Wageningen, the Netherlands/Rønde, Denmark.

Marion GM, Henry GHR, Freckman DW, Johnstone J, Jones G, Jones MH, Levesque E, Molau U, Molgaard P, Parsons AN, Svoboda J, Virginia RA

(1997) Open-top designs for manipulating field temperature in high-latitude ecosystems *Global Change Biology*, **3**, 20-32.

Marsh AS, Arnone JA, Bormann BT, Gordon JC (2000) The role of *Equisetum* in nutrient cycling in an Alaskan shrub wetland. *Journal of Ecology*, **88**, 999-1011.

Matthews JV, Ovenden LE (1990) Late Tertiary plant macrofossils from localities in Arctic Sub-Arctic North-America - a review of the data. *Arctic*, **43**, 364-392.

Maxwell B (1992) Arctic climate: Potential for change under global warming. In: *Arctic Ecosystems in a Changing Climate An ecophysiological perspective* (eds Chapin FS, Jefferies RL, Reynolds JF, Shaver GR, Svoboda J) pp 11-34 Academic Press.

McNaughton SJ (1983) Compensatory plant-growth as a response to herbivory. *Oikos*, **40**, 329-336.

Milchunas DG, Lauenroth WK (1993) Quantitative effects of grazing on vegetation and soils over a global range of environments. *Ecological Monographs*, **63**, 327-366.

Nielsen OJ, Nicolaisen FM, Bacher C, Hurley MD, Wallington TJ, Shine KP (2002) Infrared spectrum and global warming potential of SF_5CF_3. *Atmospheric Environment*, **36**, 1237-1240.

Norsk Polarinstitutt (2003) Adventdalen. Norsk Polarinstitutt. Tromso, Norway.

Oksanen L, Fretwell SD, Arruda J, Niemela P (1981) Exploitation ecosystems in gradients of primary productivity. *American Naturalist*, **118**, 240-261.

Olofsson J (2006) Plant diversity and resilience to reindeer grazing. *Arctic Antarctic and Alpine Research*, **38**, 131-135.

Olofsson J, Stark S, Oksanen L (2004) Reindeer influence on ecosystem processes in the tundra. *Oikos*, **105**, 386-396.

Paige KN (1992) Overcompensation in response to mammalian herbivory - from mutualistic to antagonistic interactions. *Ecology*, **73**, 2076-2085.

Petit JR, Jouzel J, Raynaud D, Barkov NI, Barnola IM, Basile I, Bender M, Chappellaz J, Davis M, Delaygue G, Delmotte M, Kotlyakov VM, Legrand M, Lipenkov VY, Lorius C, Pepin L, Ritz C, Saltzman E, Stievenard M (1999) Climate and atmospheric history of the past 420,000 years from the Vostok ice core, Antarctica. *Nature*, **399**, 429-436.

Pohl S, Marsh P (2006) Modelling the spatial-temporal variability of spring snowmelt in an Arctic catchment. *Hydrological Processes*, **20**, 1773-1792.

Robertson DG, Slack RD (1995) Landscape change and its effects on the wintering range of a lesser snow goose *Chen caerulescens caerulescens* population - a review. *Biological Conservation*, **71**, 179-185.

Rosenthal JP, Kotanen PM (1994) Terrestrial plant tolerance to herbivory. *Trends in Ecology and Evolution*, **9**, 145-148.

Sakamaki Y, Ino Y (2002) Influence of shade timing on an *Equisetum arvense L.* population. *Ecological Research*, **17**, 673-686.

Shevtsova A, Nilsson MC, Gallet C, Zackrisson O, Jaderlund A (2005) Effects of long-term alleviation of nutrient limitation on shoot growth and foliar phenolics of *Empetrum hermaphroditum*. *Oikos*, **111**, 445-458.

Siegismund HR, Philipp M (1999) The genus *Dryas* on Svalbard: morphological and genetic evidence for a single species, *Dryas octopetala* L. - *Det Norske Videnskaps-Akademi. Klasse, Skrifter, Ny serie*, **38**, 269-279.

Smith SD, Huxman TE, Zitzer SF, Charlet TN, Housman DC, Coleman JS, Fenstermaker LK, Seemann JR, Nowak RS (2000) Elevated CO_2 increases productivity and invasive species success in an arid ecosystem. *Nature*, **408**, 79-82.

Srivastava DS, Jefferies RL (1996) A positive feedback: Herbivory, plant growth, salinity, and the desertification of an Arctic salt-marsh. *Journal of Ecology*, **84**, 31-42.

Vitousek PM, Mooney HA, Lubchenco J, Melillo JM (1997) Human domination of Earth's ecosystems. *Science*, **277**, 494-499.

Walker NA, Henry HAL, Wilson DJ, Jefferies RL (2003) The dynamics of nitrogen movement in an Arctic salt marsh in response to goose herbivory: a parameterized model with alternate stable states. *Journal of Ecology*, **91**, 637-650.

Webster MS, Marra PP, Haig SM, Bensch S, Holmes RT (2002) Links between worlds: unraveling migratory connectivity. *Trends in Ecology and Evolution*, **17**, 76-83.

WMO World Data Centre for Greenhouse Gases (2006) Japan Meteorological Agency in Cooperation with the world meteorological Organization, Tokyo Japan. http://gaw.kishou.go.jp/wdcgg.html

Zellmer ID, Clauss MJ, Hik DS, Jefferies RL (1993) Growth responses of Arctic graminoids following grazing by captive lesser snow geese. *Oecologia*, **93**, 487-492.

CHAPTER 2

RESPONSE OF *EQUISETUM ARVENSE* TO WARMING AND GOOSE HERBIVORY IN ADVENTDALEN, SVALBARD: HOW DO HORSETAILS COPE?[1]

Introduction

The potential consequences of rapidly warming Arctic tundra vegetation have been studied for more than a decade (Chapin *et al.* 1995). Numerous experimental studies have demonstrated various effects of warming (e.g. ITEX experiments; Arft *et al.* 1999), however, most studies have examined warming exclusively or in combination with a limited number of other factors, primarily fertilizer addition or increased carbon dioxide concentrations (e.g. Veteli *et al.* 2002; Van Wijk *et al.* 2004; Deslippe *et al.* 2005; Zvereva and Kozlov 2006). Only a few studies have considered the potential interactions between changes in plant productivity associated with warming and herbivory (e.g. Veteli *et al.* 2002; Flynn *et al.* 2006). In virtually all habitats herbivores of some variety consume vegetation, interacting with and inducing responses in the plants they graze and their neighbours (Mulder and Ruess 1998; Danell and Bergström 2002). Herbivores have been important ecological agents under recent historic climatic conditions and will continue to act on plant productivity and species composition under the predicted warmer climatic conditions, therefore it is important to

[1] A version of this chapter is in preparation for publication with the following co-authors: I.S. Jónsdóttir, E.J. Cooper, and D.S. Hik.

understand how plants respond to warming when they are also under herbivory stress.

Studies that have examined plant-herbivore interactions under warmer temperatures have focused predominantly on invertebrate herbivores (e.g. Veteli *et al.* 2002; Roy *et al.* 2004; Flynn *et al.* 2006; Zvereva and Kozlov 2006), historically grazed landscapes (Karlsson *et al.* 2004), or artificial clipping (Klein *et al.* 2005). The paucity of studies on vertebrate herbivores and warming is due in part to the methods used to experimentally warm vegetation. Chamber-type designs act as a physical barrier to herbivores (Marion *et al.* 1997; Richardson *et al.* 2000). Consequently, relatively little is known about the effects of vertebrate herbivores on vegetation under climate-change conditions.

In this study we examined how *Equisetum arvense* responds to warming treatments under two levels of goose herbivory. *Equisetum* spp. are a unique and important source of forage for a variety of fauna including barnacle geese (Fox and Bergerson 2005), lesser snow geese (Brackney and Hupp 1993), trumpeter swans (Grant *et al.* 1994), red-deer (Chen *et al.* 1998), and are even consumed by grizzly bears (McLellan and Hovey 1995). Sphenophytes dominated during the Carboniferous with large arborescent growth forms, but today are reduced to 15-20 species within the *Equisetum* genus occurring on all continents except Australia (Gifford and Foster 1989). Despite their ancient lineage and ubiquity, very little is known about how these plants respond to herbivory.

Previous studies have shown that *Equisetum* spp. are highly selected for by herbivores (Brackney and Hupp 1993; Grant *et al.* 1994), but have not

examined how plants that have been grazed respond to herbivory. Some *Equisetum* spp. can accumulate minerals from the soil (Brooks *et al.* 1981) and thus have very high concentrations of macronutrients such as P, Fe, Mn, Mg, Ca and K (Auclair 1979). These high concentrations of macronutrients can be related to medicinal properties in the *Equisetum* species, which have been used medicinally by people in many parts of the world, including Peru, Morocco, Turkey, Mongolia, and Northern British Columbia, Canada (Mackinnon *et al.* 1992; Magmar and Aniya 2000; Mekhifi *et al.* 2004; Uzun *et al.* 2004; Kloucek *et al.* 2005). These medicinal properties and high macronutrient levels may be some of the reasons *Equisetum* spp. are preferred by herbivores.

Sphenophytes have a unique growth form that is characterized by jointed stems often with whorls of branches at the nodes. Reproductive shoots are distinct from vegetative shoots, however the dominant mode of growth and dispersal is through rhizome elongation (Sakamaki and Ino 2004). The belowground rhizome systems of the *Equisetum* spp. in northern ecosystems are ecologically important (Marsh *et al.* 2000). Like many perennials, resources for the following year's growth are accumulated and stored in rhizomes and tubers (Sakamaki and Ino 2002). These rhizomes are highly regenerative (Cloutier and Watson 1985). In tundra environments, they grow deeper than those of most other species and act as nutrient pumps, bringing nutrients from regions unattainable by most plants to the surface where the aboveground parts degrade and decompose quickly or are eaten by herbivores (Marsh *et al.* 2000).

Consequently, when herbivores forage on *Equisetum* spp. they are consuming nutrients from deep in the soil.

These characteristics set *Equisetum* spp. apart from the growth forms and functional groupings typically allocated by climate change researchers as they are neither graminoids, nor conventional forbs (Arft *et al.* 1999; Van Wijk *et al.* 2004). In addition, the majority of warming studies are conducted in easily accessible dry tundra where these species are rare, while the wet tundra areas that the *Equisetum* spp. inhabit abundantly are relatively ignored. Nevertheless, *Equisetum arvense* is circumpolar, commonly occurring in arctic wetlands. Other members of the *Equisetum* genus have been shown to respond to temperature, with an increase in shoot length and density, especially in the early growing season (Solander 1983; Ojala *et al.* 2002). This is similar to the response of some graminoid and forb species that increase leaf length and/or biomass when warmed (Molgaard and Christensen 1997; Stenström and Jónsdóttir 1997; Arft *et al.* 1999). Despite these similarities, the growth form of *E. arvense* is not represented among the classic functional types and thus predictions of how vegetation will respond to rapid warming made through the classic functional groups may not be applicable to *E. arvense.*

In this study we examined the response of *E. arvense* to barnacle goose (*Branta leucopsis)* herbivory under ambient temperature conditions and under warmer temperature conditions enhanced by open-topped chambers in a wet tundra area located in Adventdalen, Svalbard, Norway (2003-2005). We predicted (1) that *E. arvense* would be preferred over the other dominant species; (2) that

rhizome belowground resources would remain unaffected by herbivory as the deep nutrient pump could act as a buffer supplying nutrients for rapid regrowth; and (3) that warming would increase shoot length, branch length and shoot number, but that herbivory would have an opposing effect.

Methods

Study site

This study was conducted from 2003 to 2005 in Adventdalen, on the island of Spitsbergen, Norway (78°63'N, 15°22'W, elevation 25-50m above sea level). Adventdalen is a large valley extending from the Isfjorden fiord. Only a few geese breed in the valley, however they use the area for feeding briefly after their arrival on their way to the breeding sites in mid May to early June and again prior to their departure in late August. The study site is located approximately 10 km from the fiord and consisted of wet tundra vegetation where *E. arvense (L.)* and *Dupontia fisheri* (*R. Br.)* are the dominant vascular plant species and *Calliergon richardsonii (Mitt.)* is the dominant moss species. The wet tundra is maintained by constant snow and ice melt off nearby mountains and glaciers. The study site melts out in early to mid June, after the goose spring migration. Caribou (*Rangifer tarandus platyrhynchus*) are resident in the area and grazed the study site prior to manipulations at densities in the range of 3.7 – 5.4 animals/ km^2 (Wegener and Odasz-Albrigtsen 1998).

Experimental Design

We used a factorial random block design with two main effects: herbivory (0 hours, 1 hour, 5 hours) and temperature (ambient and elevated). Five blocks with six $2m^2$ plots for each treatment or control were constructed in late summer 2002. In early summer 2003 treatments were randomly assigned to the plots. Increased temperatures associated with climate change were simulated with open-topped chambers (OTCs) that raised the temperature inside the chamber (Marion *et al.* 1997; see Appendix A). OTCs are typically employed on dry tundra, rather than wet tundra. As a result of moss trampling and compaction, we found OTCs more effectively warmed the heavily grazed plots compared to the ungrazed plots (Appendix A for details). We simulated two intensities of grazing by placing two captive barnacle geese (*Branta leucopsis*) on the $2m^2$ plots for either one hour or five hours at each grazing event. The one hour grazing treatment falls within the natural range of grazing pressures of barnacle geese on wet tundra in Svalbard and is representative of normal grazing pressure (Kuijper *et al.* 2006). The five hour treatment represented a 3.7 increase in grazing intensity compared to normal conditions (Kuijper *et al.* 2006). OTCs were removed for the duration of the grazing event. In all years a grazing event took place in early to mid July at the beginning of the growing season. In 2003 and 2004 a second grazing event was conducted in early August after the peak-growing season.

In addition to the main experiment, an unreplicated set of plots were established as a grazing gradient, where two geese were placed on plots for 0.5, 2,

3, 4, or 7 hours. The 0, 1 and 5 hour treatments were taken from an adjacent control block of the main experiment.

Measurements

We made detailed measurements of *E. arvense* shoot densities, ramet growth responses and harvested rhizomes to use as an estimate of population level changes, productivity and nutrient reserves, respectively (see Figure 1). We estimated *E. arvense* shoot densities by counting the number of shoots in a 22.5cm x 22.5cm area in each plot before they were grazed in 2003, and before and after they were grazed in 2004 and 2005. In 2004 and 2005, this enabled us to identify the number of shoots that were grazed. We also measured shoots of the other dominating species, *Dupontia fisheri* in 2004 and 2005. In 2004, we marked, and then measured, ten vegetative aerial shoots in each plot on a weekly basis from snowmelt until senescence, a total of 12 weeks in 2004. Each shoot was labelled with a plastic ring made from a drinking straw. We recorded the height of each aerial stem from the basal node to tip and also measured the lowest, longest branch length of each shoot (Figure 2 - 1). In 2005, the heights of 10 target shoots per plot were measured early in the spring, prior to the grazing event, after the grazing event and in the ungrazed treatments, in midsummer. Branch length was not measured in 2005.

At the end of August 2005, five *E. arvense* rhizome segments from each high and ungrazed grazing treatment were randomly harvested. The rhizome segment mass:length ratio is a proxy for the size of belowground stores and new,

un-established ramets are an estimate of reserves invested in future growth. Rhizomes were washed in the field, and stored in a refrigerator until processed. They were then washed, trimmed at the junction with a branching rhizome, and their length was measured. Un-established ramets that had not reached the surface were counted, removed, measured, and combined with the other un-established ramets from a single rhizome segment. Aerial stems that were above the surface were counted and removed. Rhizome segments and un-established aerial stems were dried at 70°C for at least 72 hours, placed in a desiccator to cool and then weighed. Rhizome segments were weighed to the nearest tenth of a milligram and un-established ramets were weighed to the nearest microgram.

Statistics

Forage preference

Foraging preferences of geese between *Dupontia fisheri* and *Equisetum arvense* were analysed using a 3-way log-linear contingency table analysis (VasserStats, Lowry 2001). The number of shoots grazed and left ungrazed in the grazing gradient were compared using the first 5 of the 7 grazing periods.

Time series measurements (shoot density, stem height and branch length)

The mixed procedure in SAS version 8.1 (SAS Institute Inc. 1999) was used to analyze annual variation in shoot densities, stem heights prior to grazing events, branch lengths prior to grazing events, and senescence. Shoot densities were square root transformed after adding 0.375 to each value before transformation

(Zar 1999). An unstructured covariance structure was assumed for yearly shoot density measurements, while autoregressive covariance structures were assumed for both stem heights and branch lengths. In all analyses, maximum likelihood estimation was used and degrees of freedom were calculated using the Satterthwaite method (Kragten 1994). Temperature, grazing, and time, were treated as fixed effects and block was treated as a random effect. In the stem height and branch length analyses, plots were nested within block and treated as random factors and individual plants were treated as repeated subjects. In the stem height analysis, time (week) was nested within year. Treatment combination (plot) was considered the repeated subject in the shoot density analysis. The senescence analysis was conducted for the ungrazed treatments in 2004 only. Type three sums of squares were used.

Belowground rhizomes

Rhizome segments from 2005 were analysed using the mixed procedure in SAS version 8.1 (1999). Mass was treated as a dependent variable. Grazing and temperature were treated as fixed effects, and block, treatment combination (plot) nested within block, and rhizome length was treated as random effects. Segment lengths and masses were log transformed. Lengths and masses of un-established ramets were analysed similarly to the rhizome segments. Because un-established ramets were not measured individually, the total mass of all un-established ramets in a rhizome segment was used as the dependent variable and the combined length was treated as a random factor. The number of un-established ramets per segment

was used as a covariate. Mass, length and number of un-established ramets were log transformed to achieve normality. Main effect covariate interactions were removed from analyses when not significant. The mean mass and the mean length of un-established ramets were analysed similarly to rhizome segments but without a covariate to test for differences in length. The total masses and the total lengths of un-established ramets were divided by the number un-established ramets on a given rhizome segment.

Results

Susceptibility to herbivory

Equisetum arvense was selected over *Dupontia fisheri* in the grazing gradient trials in both 2004 and 2005 (in 2004 Graze × Species × Hrs grazed $G_{(2)}^2$=402, P<0.0001; in 2005 Graze × Species × Hrs grazed $G_{(2)}^2$=241.84, P<0.0001). In both years, after two hours of grazing more than 95% of *E. arvense* shoots had been grazed compared with fewer than 20% of *D. fisheri* shoots (Figure 2 - 2).

Belowground treatment effects

Rhizome mass was negatively affected by herbivory (Graze $F_{(1,\ 14.4)}$=9.72, P=0.0073) and independent of temperature (Temperature $F_{(1,\ 13.2)}$=0.29, P=0.5977) (Figure 2 - 3). This pattern was also observed in the un-established ramets (Graze $F_{(1,\ 14.4)}$=6.86, P=0.0199; Temperature $F_{(1,\ 13.7)}$=2.51, P=0.1360; Number of un-established ramets $F_{(1,\ 60.6)}$=3.13, P=0.0818). Neither the mean mass nor the mean length of un-established ramets was significantly affected by treatments.

Shoot density

Intense grazing over the three years had a significant negative effect on the number of shoots produced each year (Graze × Year Interaction $F_{(4, 85)}$=2.69, P=0.0369). Year was also significant ($F_{(2, 85)}$=3.91, P=0.0237). There was a non-significant interaction trend between temperature and grazing ($F_{(2, 85)}$=2.69, P=0.0737), indicating increased shoot densities in the ungrazed, OTC treatments compared to the ungrazed, ambient treatment, but no warming effect in the herbivory treatments (Figure 2 - 4).

Aboveground measurements

The effects of grazing and warming had opposing effects on spring growth rates. Grazed shoots grew more slowly, while warmed shoots grew more rapidly than plants in control plots in both 2004 and 2005 (Table 2 - 1; Figure 2 - 5).

In addition, the basal branch lengths of *E. arvense* shoots responded to temperature. The temperature × time interaction was significant ($F_{(2, 522)}$=19.91, P<0.0001), as were the main effects of time ($F_{(2, 522)}$=762.76, P<0.0001) and temperature ($F_{(1, 25.1)}$=13.63, P=0.0011). Shoots growing in OTCs had longer branch lengths than those growing in ambient conditions prior to the first grazing event in 2004 (Figure 2 - 6), however, by the end of summer branch lengths in ungrazed-ambient plots had caught up to branch lengths in the ungrazed-warmed plots (Ungrazed treatments only: $F_{(1,5)}$=1.52, P=0.2730). Grazing did not significantly affect branch length prior to the grazing event.

Discussion

Susceptibility to herbivory

Geese select forage based upon their nutrient requirements, season, time and/or energy required to harvest plants, and the nutrients in those plants (Owen 1972; Cadieux *et al.* 2005). In our experiment, barnacle geese consistently selected *Equisetum arvense* over *Dupontia fisheri*, the other dominant species at our site, which was consistent with our predictions. Presence of *Equisetum* spp. is documented in the diets of barnacle geese (Prop and Vulink 1992; Fox and Bergensen 2005) as well as other herbivorous waterfowl such as snow geese, Canada geese and trumpeter swans (Prevett *et al.* 1985; Brackney and Hupp 1993; Grant *et al.* 1994). Thomas and Prevett (1982) found young *Equisetum fluviatile* aerial stems were high in protein, and that amino acids occurred in proportions comparable to optimal proportions in commercial goose feed when shoots were young, at the beginning of the growing season. However as shoots aged they became less nutritious. Thomas and Prevett (1982) hypothesized that the high phosphorous, calcium and other nutrient concentrations are particularly beneficial during egg production and during the gosling growth period. This may explain the preference of barnacle geese for *E. arvense*. *E. arvense* was likely more susceptible to herbivory than other species to grazing by barnacle geese in the spring and early summer for reasons outlined above.

Belowground dynamics

Equisetum arvense has a massive belowground rhizome system (Marsh *et al.* 2000). In temperate areas, rhizome densities of $80m/m^2$ have been documented (Sakamaki and Ino 2004). In the Arctic, *Equisetum* spp. rhizomes and roots extend deeper than those of many other species, enabling utilization of resources unattainable by other species (Marsh *et al.* 2000). This extensive rhizome system may be a source of nutrients that can enable recovery from herbivory. Roots and rhizome parameters are difficult to measure (Eissenstat *et al.* 2000), especially in clonal species, however our limited estimate of belowground reserves indicated strong differences between the ungrazed treatments and the 5 hour grazing treatments. Contrary to what we hypothesized, we observed significantly less mass per unit length in the grazed treatments indicating that these belowground resources were indeed being depleted and new ramets had fewer resources allocated to them. The complete loss of nearly all aboveground biomass at the beginning of the growing period over three growing seasons resulted in a net decline of reserves. The below-ground nutrient pump did not feed a compensatory mechanism thus a net loss of below-ground resources was observed.

Shoot density

Shoot densities were estimated over three years (2003-2005). There was large variability within treatments, in part because these data were collected in a small 22.5 x 22.5 cm area within each plot. Despite this, our measurements

documented a consistent decline in shoot densities over the three year period in the intense (5 hour) grazing treatments. This decline did not occur in the 1 hour grazing treatment. Fewer shoots were grazed in the 1 hour treatment (approx. 75% compared with 98% in the 5 hour treatments in 2004). In addition, the extent they were grazed varied. In the 5 hour treatment, essentially all shoots were completely removed: geese pulled the base of the aerial shoot out of the soil and consumed it. In the 1 hour treatment, geese left 2.1 +/- 0.2 cm of stem. Aerial stems with a height of 2 cm retain at least one branch whorl, and their meristems from which new shoots can re-grow in subsequent years.

Aboveground dynamics

The decline in belowground reserves in grazed treatments resulted in the reduced aboveground growth we observed in 2005. At the beginning of the growing season, plants in grazed treatments had slower vertical growth than those in ungrazed treatments; plants in the ungrazed plots grew the fastest and those in the 5 hour grazing treatments grew the slowest, while the 1 hour treatments had an intermediate growth rate. The grazing events occurred in the early summer, and since nearly all shoots in the 5 hour grazing treatment were removed we do not know if the maximum stem heights attained by the various treatments differed. Most detailed work on the response of plants to herbivory in the Arctic has focused on graminoids (e.g. Gauthier *et al.* 1995; Wegener and Odasz 1997; Mulder and Ruess 1998). Graminoids have basal meristems and are thus able to recover from herbivory by producing new leaves following grazing (Johnson and

Parsons 1985). *Equisetum arvense* does not have such compensatory strategies and grazing results in the loss of apical meristems which prevents further growth within the same season for a specific ramet.

Temperature effects

Increased temperature had an opposite effect to grazing on aboveground growth: plants growing in OTCs had faster vertical growth in the early growing season. Branch lengths also responded to warming at the beginning of the season, but were unaffected by grazing. This is interesting as we might expect grazing to delay branch length growth as it delays stem growth. Since this was not the case, it is likely that branches begin to develop as a response to temperature and not when a plant achieves a certain size.

Although warming affected both stem height and the onset of branch whorl production at the beginning of the growing season, it did not result in larger plants. Neither final stem height, nor branch lengths were significantly larger in warmed treatments at the end of July. This indicates that the maximum size *E. arvense* attains is not altered by warming and that warming simply accelerates growth at the beginning of the growing season. Senescence was not affected by OTCs which conflicts with the findings of Marchand *et al.* (2004), but is in agreement with the general findings in the Arctic (Arft *et al.* 1999) and in temperate areas (Keskitalo *et al.* 2005), where the onset of senescence is predominantly controlled by photoperiod, and not temperature.

Warming did not affect shoot densities, nor susceptibility to herbivory, however increases in atmospheric CO_2 coupled with warmer temperatures have been shown to alter the C:N ratios and defensive compounds in some plants (Veteli *et al.* 2002; Jónsdóttir *et al.* 2005; Zvereva and Kozlov 2006). These changes can, in the future, alter plant susceptibility to herbivory.

Interactions between grazing and temperature

Changes in climate, resulting in warmer temperatures and altered precipitation patterns, can cause immediate effects on primary producers, which, in turn can potentially affect those species interacting with them (ACIA 2005; IPCC 2001). Visser and Both (2005) document several cases where inter-trophic interactions became mis-timed as a result of climate change, resulting from different control cues. We have shown that growth of *Equisetum arvense* responded to warmer temperatures by accelerating phenology. This species is an important food source for breeding waterfowl and their growing offspring at the beginning of the season, therefore, it is important to consider how both waterfowl and *Equisetum arvense* respond temporally to climate change. The exact mechanisms triggering the spring migration in avian species are not fully understood, however endogenous elements responding to changes in photoperiod (Berthold and Terrill 1991) and fat deposition (Prop *et al.* 2003) are believed to be important. Photoperiod is not affected by climate change, therefore herbivorous waterfowl arriving at approximately the same time each year can become mis-timed with their vegetation resources. Migrating waterfowl have evolved with natural variability

in time of snowmelt and consequent plant phenology, however climate change can increase that variability outside of the familiar ranges. Climate change will not necessarily result in mis-timing and can have additional benefits in increased biomass: although increases in early season growth were in the order of millimetres, these small amounts accumulate rapidly when large areas are considered.

Equisetum arvense is an important species in wet tundra vegetation, but has largely been ignored in multi-species climate change studies. It is an important forage plant and susceptible to changes in climate. This study demonstrates that the growth of *E. arvense* responds to both herbivory and warming and that these effects are in opposite directions. Grazing tends to reduce growth and aerial stem production at the beginning of the following summer due to loss of belowground reserves, while warming tends to increase productivity. Plants that were both grazed and warmed tended to produce about as much early season biomass as ungrazed, un-warmed plants. As such, *E. arvense* is a responsive species, responding to changes in both climatic conditions as well as inter-trophic interactions.

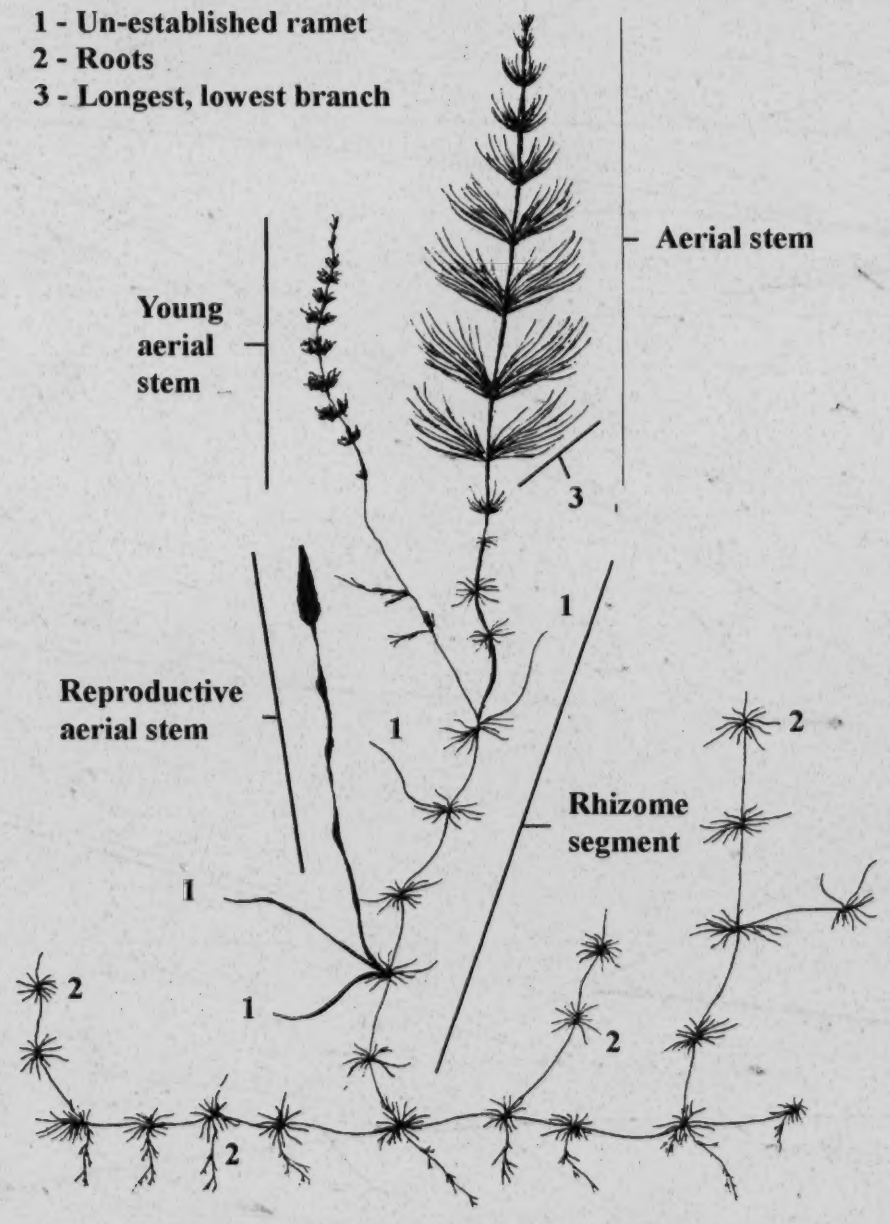

Figure 2-1: *Equisetum arvense* diagram. One mature aerial stem, one young aerial stem, and one reproductive aerial stem. Rhizome segments, un-established ramets, roots and branches also shown. Drawn by Mandana Rahbari.

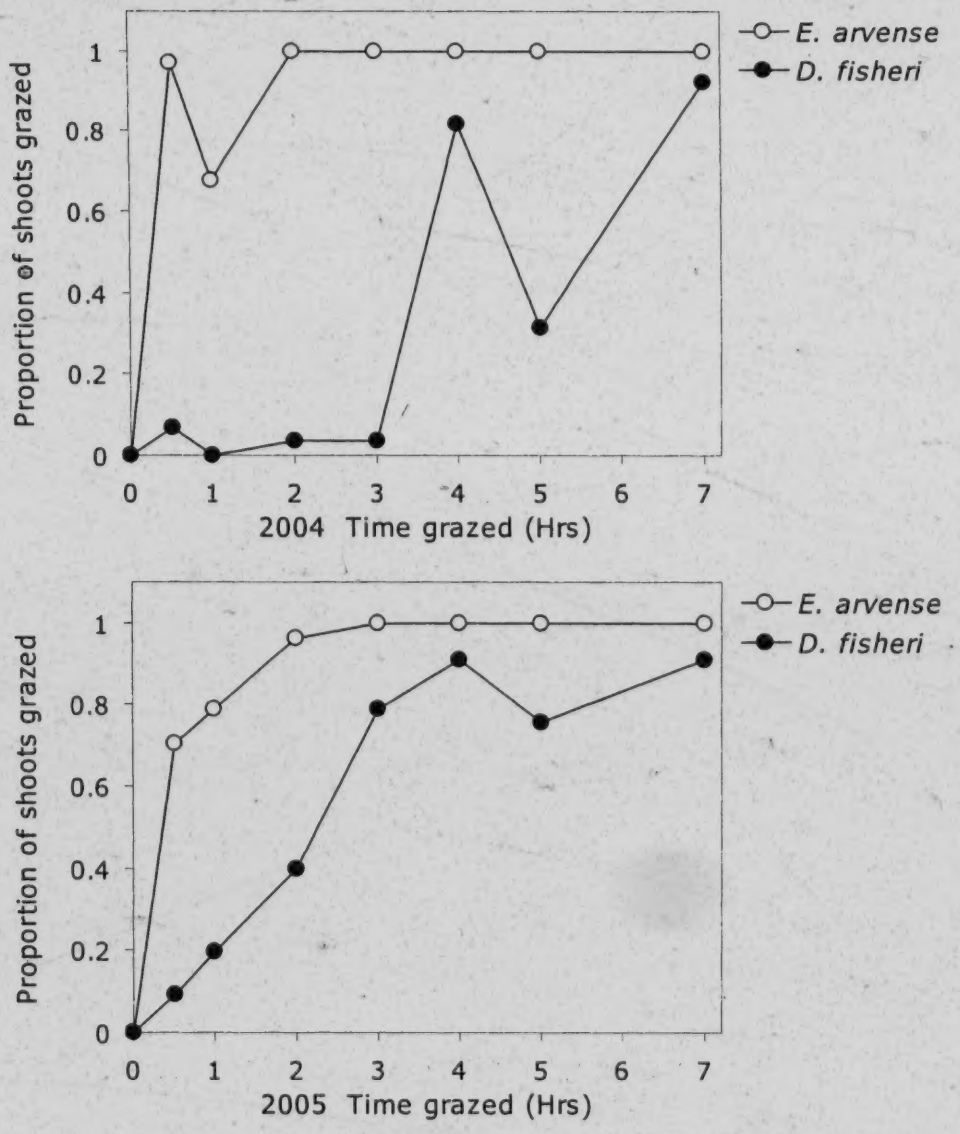

Figure 2-2: Proportion of grazed *Equisetum arvense* and *Dupontia fisheri* shoots in a 22.5cm^2 quadrat in the grazing gradient trials in 2004 (first panel) and 2005 (second panel). *E. arvense* was highly preferred in both years.

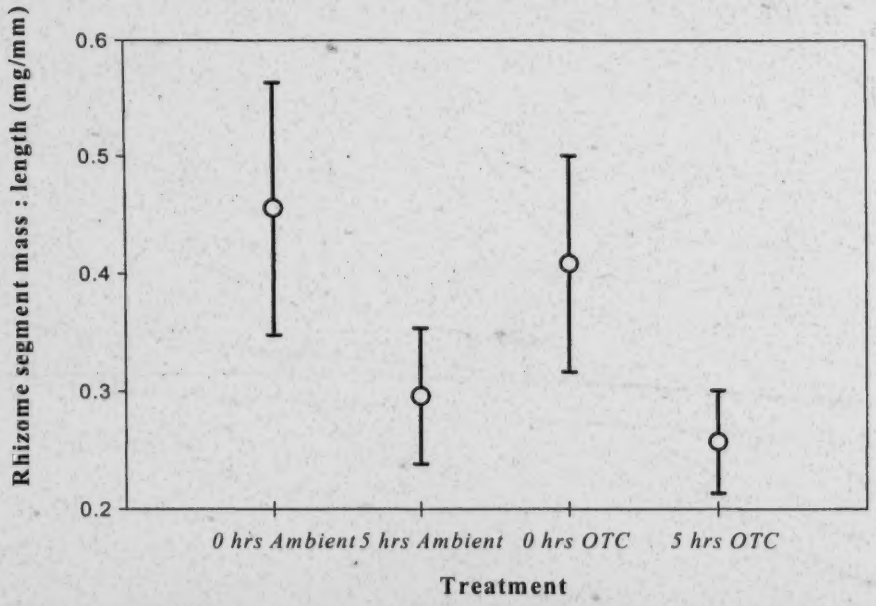

Figure 2-3: Rhizome segment mass : length ratio of intensely grazed treatments and ungrazed treatments at two temperature levels (mean +/- 95% confidence intervals). Goose herbivory significantly reduced rhizome mass per segment length.

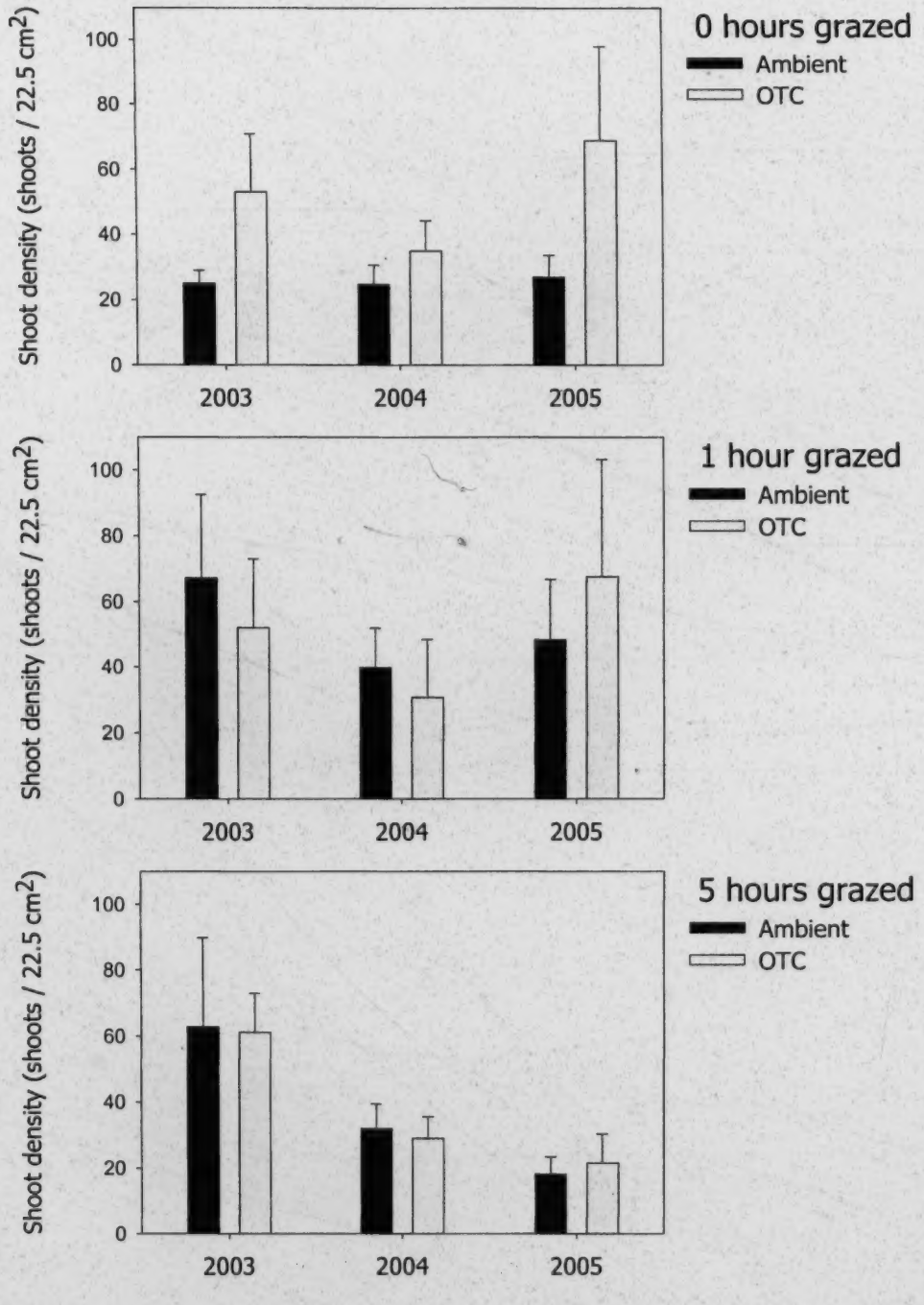

Figure 2-4: *Equisetum arvense* shoot densities 2003-2005, grouped by grazing treatment (Mean +/- 1 SE). Grazing in the 5 hour plots caused a significant reduction in shoot density over the three year period.

Table 2-1: *Equisetum arvense* stem heights prior to grazing 2004-2005. Measurements were taken on the length of the stem at weekly intervals up until the grazing events. Stems grew significantly slower in grazed plots over time, but grew significantly faster in warmed plots over time.

Effect	Num DF	Den DF	F Value	Pr > F
Temperature	1	25.7	3.96	0.0574
Graze	**2**	**25.7**	**14.50**	**<0.0001**
Time	**4**	**920**	**877.37**	**<0.0001**
Temperature × Graze	2	25.7	0.51	0.6036
Temperature × Time	**4**	**920**	**3.86**	**0.0040**
Graze × Time	**8**	**920**	**2.43**	**0.0134**
Temperature × Graze × Time	8	920	0.59	0.7856

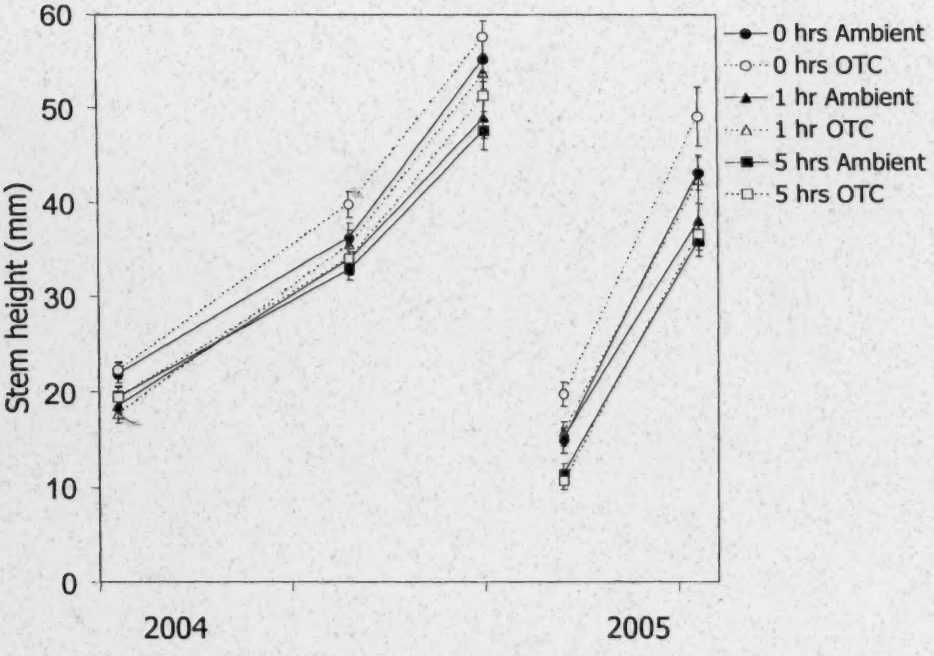

Figure 2-5: *Equisetum arvense* stem heights in 2004 and 2005 before the herbivory event (mean +/- 1 SE). Within each year, measurements are 7-10 days apart.

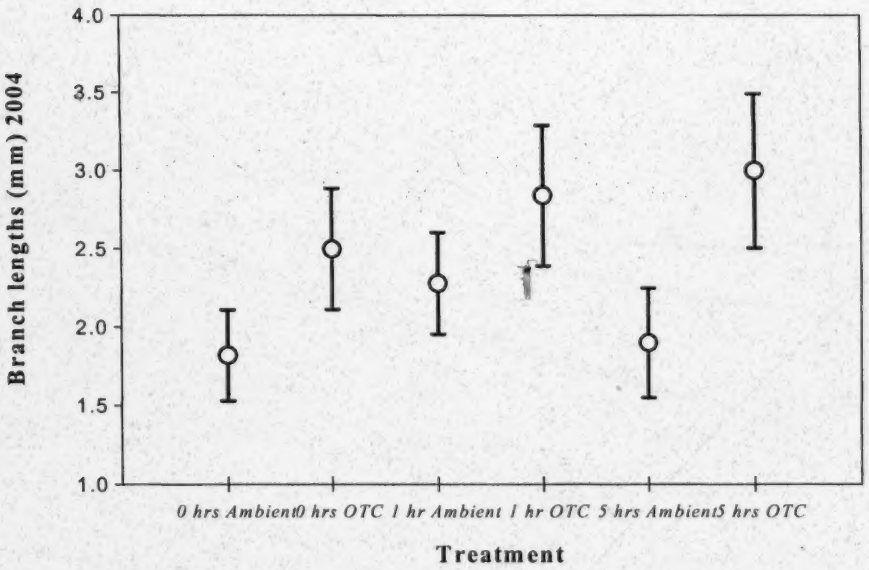

Figure 2-6: *Equisetum arvense* branch lengths 28-29 June 2004, prior to the grazing event (mean +/- 95% CI).

Literature Cited

ACIA (2005) Arctic Climate Impact Assessment. Cambridge University Press, Cambridge.

Arft AM, Walker MD, Gurevitch J, Alatalo JM, Bret-Harte MS, Dale M, Diemer M, Gugerli F, Henry GHR, Jones MH, Hollister RD, Jónsdóttir IS, Laine K, Levesque E, Marion GM, Molau U, Molgaard P, Nordenhall U, Raszhivin V, Robinson CH, Starr G, Stenstrom A, Stenstrom M, Totland O, Turner PL, Walker LJ, Webber PJ, Welker JM, Wookey PA (1999) Responses of tundra plants to experimental warming: Meta-analysis of the international tundra experiment. *Ecological Monographs*, **69**, 491-511.

Auclair AND (1979) Factors affecting tissue nutrient concentrations in a *Scirpus-Equisetum* Wetland. *Ecology*, **60**, 337-348.

Berthold P, Terrill SB (1991) Recent advances in studies of bird migration. *Annual Review of Ecology and Systematics*, **22**, 357-378.

Brackney AW, Hupp JW (1993) Autumn diet of lesser snow geese staging in Northeastern Alaska. *Journal of Wildlife Management*, **57**, 55-61.

Brooks RR, Holzbecher J, Ryan DE (1981) Horsetails (*Equisetum*) as indirect indicators of gold mineralization. *Journal of Geochemical Exploration*, **16**, 21-26.

Cadieux MC, Gauthier G, Hughes RJ (2005) Feeding ecology of Canada geese (*Branta Canadensis interior*) in sub-arctic inland tundra during brood-rearing. *Auk*, **122**, 144-157.

Chapin FS, Shaver GR, Giblin AE, Nadelhoffer KJ, Laundre JA (1995) Responses of Arctic tundra to experimental and observed changes in climate. *Ecology*, **76**, 694-711.

Chen HP, Ma JZ, Li F, Sun ZW, Wang HA, Luo LY, Li F (1998) Seasonal composition and quality of red deer *Cervus elaphus* diets in northeastern China. *Acta Theriologica*, **43**, 77-94.

Cloutier D, Watson AK (1985) Growth and regeneration of field horsetail (*Equisetum Arvense*). *Weed Science*, **33**, 358-365.

Danelle K, Bergstrom R (2002) Mammalian herbivory in terrestrial environments. In: *Plant-Animal Interactions An Evolutionary Approach* (eds Herrera CM, Pellmyr O), pp. 107-131. Blackwell Science, Cornwall.

Deslippe JR, Egger KN, Henry GHR (2005) Impacts of warming and fertilization on nitrogen-fixing microbial communities in the Canadian High Arctic. *FEMS Microbiology Ecology*, **53**, 41-50.

Eissenstat DM, Wells CE, Yanai RD, Whitbeck JL (2000) Building roots in a changing environment: implications for root longevity. *New Phytologist*, **147**, 33-42.

Flynn DFB, Sudderth EA, Bazzaz FA (2006) Effects of aphid herbivory on biomass and leaf-level physiology of *Solanum dulcamara* under elevated temperature and CO2. *Environmental and Experimental Botany*, **56**, 10-18.

Fox AD, Bergersen L (2005) Lack of competition between barnacle geese *Branta leucopsis* and pink-footed geese *Anser brachyrhynchus* during the pre-breeding period in Svalbard. *Journal of Avian Biology*, **36**, 173-178.

Gauthier G, Hughes RJ, Reed A, Beaulieu J, Rochefort L (1995) Effect of grazing by greater snow geese on the production of graminoids at an arctic site (Bylot Island, NWT, Canada). *Journal of Ecology*, **83**, 653-664.

Gifford E. M., A. S. Foster. (1989) Sphenophyta. In Morphology and Evolution of Vascular Plants 3rd edition. 1959 Freeman. 175-207.

Grant TA, Henson P, Cooper JA (1994) Feeding ecology of trumpeter swans breeding in South Central Alaska. *Journal of Wildlife Management*, **58**, 774-780.

IPCC Report (2001) IPCC Third Assessment Report – Climate Change 2001.

Johnson IR, Parsons AJ. (1985) A theoretical analysis of grass growth under grazing. *Journal of Theoretical Biology*, **112**, 345-357.

Jónsdóttir IS, Khitun O, Stenström A (2005) Biomass and nutrient responses of a clonal tundra sedge to climate warming. *Canadian Journal of Botany*, **83**, 1608–1621

Karlsson PS, Tenow O, Bylund H, Hoogesteger J, Weih M (2004) Determinants of mountain birch growth in situ: effects of temperature and herbivory. *Ecography*, **27**, 659-667.

Keskitalo J, Bergquist G, Gardestrom P, Jansson S (2005) A cellular timetable of autumn senescence. *Plant Physiology*, **139**, 1635-1648.

Klein JA, Harte J, Zhao XQ (2005) Dynamic and complex microclimate responses to warming and grazing manipulations. *Global Change Biology*, **11**, 1440-1451.

Kloucek P, Polesny Z, Svobodova B, Vlkova E, Kokoska L (2005) Antibacterial screening of some Peruvian medicinal plants used in Calleria District. *Journal of Ethnopharmacology*, **99**, 309-312.

Kragten J (1994) Calculating standard deviations and confidence intervals with a universally applicable spreadsheet technique. *Analyst*, **119**, 2161-2165.

Kuijper DPJ, Bakker JP, Cooper EJ, Ubels R, Jonsdottir IS (2006) Intensive grazing by Barnacle geese depletes High Arctic seed bank. *Canadian Journal of Botany*, **84**, *in press*

Mackinnon A, Pojar J, Coupe R. eds (1992) Horsetails. In: *Plants of Northern British Columbia*. pp. 280-284. Lone Pine Publishing, Vancouver.

Marchand FL, Nijs I, Heuer M, Mertens S, Kockelbergh F, Pontailler JY, Impens I, Beyens L (2004) Climate warming postpones senescence in High Arctic tundra. *Arctic Antarctic and Alpine Research*, **36**, 390-394.

Marion GM, Henry GHR, Freckman DW, Johnstone J, Jones G, Jones MH, Levesque E, Molau U, Molgaard P, Parsons AN, Svoboda J, Virginia RA (1997) Open-top designs for manipulating field temperature in high-latitude ecosystems. *Global Change Biology*, **3**, 20-32.

Marsh AS, Arnone JA, Bormann BT, Gordon JC (2000) The role of *Equisetum* in nutrient cycling in an Alaskan shrub wetland. *Journal of Ecology*, **88**, 999-1011.

Mclellan BN, Hovey FW (1995) The diet of grizzly bears in the Flathead River drainage of Southeastern British-Columbia. *Canadian Journal of Zoology-Revue Canadienne de Zoologie*, **73**, 704-712.

Mekhfi H, El Haouari M, Legssyer A, Bnouham M, Aziz M, Atmani F, Remmal A, Ziyyat A (2004) Platelet anti-aggregant property of some Moroccan medicinal plants. *Journal of Ethnopharmacology*, **94**, 317-322.

Molgaard P, Christensen K (1997) Response to experimental warming in a population of *Papaver radicatum* in Greenland, *Global Change Biology*, **3**, 116-124.

Mulder, CPH, Ruess RW (1998) Effects of herbivory on arrowgrass: Interactions between geese, neighboring plants, and abiotic factors. *Ecological Monographs*, **68**, 275-293.

Myagmar BE, Aniya Y (2000) Free radical scavenging action of medicinal herbs from Mongolia. *Phytomedicine*, **7**, 221-229.

Ojala A, Kankaala P, Tulonen Top (2002) Growth response of *Equisetum fluviatile* to elevated CO_2 and temperature. *Environmental and Experimental Botany*, **47**, 157-171.

Owen M (1972) Some factors affecting food intake and selection in white-fronted geese. *Journal of Animal Ecology*, **41**, 79-92.

Prevett JP, Marshall IF, Thomas VG (1985) Spring foods of snow and Canada geese at James Bay. *Journal of Wildlife Management*, **49**, 558-563.

Prop J, Black JM, Shimmings P (2003) Travel schedules to the High Arctic: barnacle geese trade-off the timing of migration with accumulation of fat deposits. *Oikos*, **103**, 403-414.

Prop J, Vulink Top (1992) Digestion by barnacle geese in the annual cycle - the interplay between retention time and food quality. *Functional Ecology*, **6**, 180-189.

Richardson SJ, Hartley SE, Press MC (2000) Climate warming experiments: are tents a potential barrier to interpretation? *Ecological Entomology*, **25**, 367-370.

Roy BA, Gusewell S, Harte J (2004) Response of plant pathogens and herbivores to a warming experiment. *Ecology*, **85**, 2570-2581.

Sakamaki Y, Ino Y (2002) Influence of shade timing on an *Equisetum arvense L.* population. *Ecological Research*, **17**, 673-686.

Sakamaki Y, Ino Y (2004) Response of non-structural carbohydrate content of belowground parts in *Equisetum arvense* according to the irradiance change during a growing season. *Journal of Plant Research*, **117**, 385-391.

SAS Institute Inc. (1999) Cary, NC, USA

Solander D (1983) Biomass and shoot production of *Carex rostrata* and *Equisetum fluviatile* in unfertilized and fertilized Subarctic lakes. *Aquatic Botany*, **15**, 349-366.

Stenstrom A, Jónsdóttir IS (1997) Responses of the clonal sedge, *Carex bigelowii*, to two seasons of simulated climate change. *Global Change Biology*, **3**, 89-96.

Thomas VG, Prevett JP (1982) The role of horsetails (*Equisetaceae*) in the nutrition of northern-breeding geese. *Oecologia*, **53**, 359-363.

Uzun E, Sariyar G, Adsersen A, Karakoc B, Otuk G, Oktayoglu E, Pirildar S (2004) Traditional medicine in Sakarya province (Turkey) and antimicrobial activities of selected species. *Journal of Ethnopharmacology*, **95**, 287-296.

Van Wijk MT, Clemmensen KE, Shaver GR, Williams M, Callaghan TV, Chapin FS, Cornelissen JHC, Gough L, Hobbie SE, Jonasson S, Lee JA, Michelsen A, Press MC, Richardson SJ, Rueth H (2004) Long-term ecosystem level experiments at Toolik Lake, Alaska, and at Abisko, Northern Sweden: generalizations and differences in ecosystem and plant type responses to global change. *Global Change Biology*, **10**, 105-123.

Vasserstats, Lowry R (2006) Poughkeepsi New York. USA.

Veteli TO, Kuokkanen K, Julkunen-Tiitto R, Roininen H, Tahvanainen J (2002) Effects of elevated CO^2 and temperature on plant growth and herbivore defensive chemistry. *Global Change Biology*, **8**, 1240-1252.

Visser ME, Both C (2005) Shifts in phenology due to global climate change: The need for a yardstick. *Proceedings of the Royal Society B-Biological Sciences*, **272**, 2561-2569.

Wegener C, Odasz AM (1997) Effects of laboratory simulated grazing on biomass of the perennial Arctic grass *Dupontia fisheri* from Svalbard: Evidence of overcompensation. *Oikos*, **79**, 496-502.

Wegener C, Odasz-Albrigtsen AM (1998) Do Svalbard reindeer regulate standing crop in the absence of predators? A test of the "exploitation ecosystems" model. *Oecologia*, **116**, 202-206.

Zar JH (1999) *Biostatistical* Analysis 4th Ed. Prentice Hall Inc.

Zvereva EL, Kozlov MV (2006) Consequences of simultaneous elevation of carbon dioxide and temperature for plant-herbivore interactions: a meta-analysis. *Global Change Biology*, **12**, 27-41.

CHAPTER 3

WARMING DELAYS MORPHOLOGICAL RESPONSES TO HERBIVORY IN *DUPONTIA FISHERI* IN ADVENTDALEN, SVALBARD[2]

Introduction

Interest in predicting the response of Arctic vegetation to climate change has intensified in recent years. Substantial evidence for rapid climate change in this century has been corroborated with evidence that such changes are already occurring at high latitudes (Houghton 2001; IPCC 2001; ACIA 2005). The sensitivity of tundra to warming has repercussions globally, in terms of the global carbon balance (Oechel *et al.* 1993), as well as regionally, where shifts in vegetation composition and function can occur (Hollister *et al.* 2005a). Understanding the response of tundra to warming is essential for predicting the fate of the 250-455 Pg of carbon stored in permafrost (Oechel and Billings 1992). Additionally, warmer temperatures and alterations in growing season length will promote growth-forms and growth of some species while inhibiting others, altering the functioning of the ecosystem. A variety of vertebrate herbivores, including ungulates, migratory waterfowl, and microtine species, are dependent on this vegetation and will be affected by any changes.

[2] A version of this chapter is in preparation for publication with the following co-authors: I.S. Jónsdóttir, E.J. Cooper, and D.S. Hik.

Warming experiments have been conducted in Arctic and alpine regions to anticipate the tundra response to climate change (e.g. Henry and Molau 1997; Marion *et al.* 1997). Comparatively uniform patches of species assemblages within a tundra landscape provide model ecosystems for identifying generalized responses to warming. Many warming studies use open-topped-chambers (OTCs) or other greenhouse-type structures to warm the tundra (e.g. ITEX experiments, Arft *et al.* 1999; Van Wijk *et al.* 2004; Walker 2005). The majority of these warming devices also act as exclosures, excluding all vertebrate herbivores (Richardson *et al.* 2000). Therefore the majority, if not all our knowledge of the tundra vegetation response to warming is based on experiments conducted in the absence of vertebrate herbivores. Although useful in determining plant responses to warmer temperatures, such conditions would be unusual in nature. Herbivores can drive vegetation dynamics by altering both species composition and productivity (e.g. Olofsson *et al.* 2001; Van der Wal *et al.* 2001; Olofsson 2006). Subjecting plants to various climate change treatments in the absence of herbivores may not be indicative of the actual responses that will occur in nature. The response of plants to warming, is known to be constrained by other variables such as nutrient availability (Shaver *et al.* 1992) and growing season length (Hollister *et al.* 2005a). It is therefore plausible that herbivory can also influence the effects of warming on vegetation.

The significant role of herbivores in structuring vegetation has generated much interest, and the general responses of plants to herbivores are fairly well understood. Strong herbivory pressures result in a diverse array of strategies and

phenotypic responses in vegetation that permit plants to tolerate and persist under intense herbivory (McIntire and Hik 2002). Some of the common responses of graminoids to grazing are increased leaf production (Kotanen and Jefferies 1987), increased tiller production (Bazely and Jefferies 1989), reduction in leaf and culm length (McNaughton 1984), and increased concentrations of leaf nitrogen (Cargill and Jefferies 1984b). Re-growth after grazing is frequently at the expense of belowground plant reserves (Beaulieu *et al.* 1996). However, in some situations, herbivores such as caribou and geese, can also increase the availability of nitrogen to plants by increasing nitrogen cycling rates through the internal processing of plant matter and consequent release in their faeces (Hik *et al.* 1991; Gauthier *et al.* 1995; Van der Wal *et al.* 2004). Nitrogen often limits plant growth in tundra environments (Marion *et al.* 1982; Cargill and Jefferies 1984a), thus the amount recycled by herbivores can be an important source for plant growth and can stimulate productivity. The proportion of net aboveground primary productivity (NAPP) that can be consumed by herbivores is significantly higher in Arctic environments, where upwards of 50% can be removed, whereas losses of around 10% are common in many other ecosystems (Jefferies *et al.* 1992). Snow geese, for example, can remove 80% of NAPP in coastal salt marshes but also increase nitrogen cycling rates (Cargill and Jefferies 1984b).

There are differences between the short and long term responses of tundra vegetation to climate change (Hollister *et al.* 2005b). Long-term responses will occur on the ecosystem level and involve plant migration, changes in nutrient composition, the formation of new species assemblages, and consequently

different functioning of the ecosystem (Callaghan *et al.* 2004; Neilson *et al.* 2005). These eventual responses are difficult to predict, as particular species interact uniquely with the distinct set of environmental characteristics and species in the localities they inhabit. However, in the short term, responses will act at the individual level resulting in transitory dynamics where species that are currently occurring adjust physiologically to changes in temperature and growing season length. Meta-analyses of sites throughout the Arctic indicate that many plants respond to elevated temperatures in the short term by increasing their aboveground vegetative growth (Arft *et al.* 1999 and Van Wijk *et al.* 2003), and specific to the High Arctic, increasing their allocation of resources to reproduction (Arft *et al.* 1999). Earlier phenology and increased leaf life spans are observed in some species (Suzuki and Kudo 2000). Graminoids responded to warming by increased vegetative growth, earlier anthesis and later senescence (Arft *et al.* 1999). However, a lack of response to temperature alone can also occur in some species (e.g. Hollister *et al.* 2005a; Wahren *et al.* 2005).

Although many of the short-term plant responses to climate change are understood in the absence of trophic interactions, little is known of how plants respond to warming when they are already stressed by vertebrate herbivores, as is frequently the case in nature. In our study we examined the response of a common wet tundra grass, *Dupontia fisheri (R. br.)*, to warming when stressed by herbivory. Warming associated with climate change was simulated using Open-topped chambers (OTCs). Captive barnacle geese were used in controlled grazing events on warmed and ambient plots to simulate two levels of herbivory. We

manipulated treatments over three summers, 2003-2005, and followed growth of *D. fisheri*, in detail over the 2004 and 2005 growing seasons.

Our experimental hypothesis is that warming mitigates the response of plants to herbivory. Specifically we predict that (1) ramets will respond to goose herbivory under ambient temperatures by (a) having aboveground productivity equal to that of ungrazed plants (exact-compensation), (b) this aboveground productivity will be at the expense of below-ground storage organs, which will become depleted as a consequence of reduced photosynthate accumulation, but maintained aboveground production, and (c) ramets will alter their morphology in response to grazing such that they produce a large number of smaller leaves. (2) In the absence of herbivores we expect ramets to respond to warming by (a) increasing aboveground productivity and below-ground productivity, (b) increasing number of leaves and leaf length, and (c) senescing earlier. In plots that are subjected to both goose herbivory and warming we expect (3) warming to mitigate the response of plants to goose herbivory, such that plants will respond to grazing in the same way as under ambient temperature, but less intensely.

Methods

Study site

This study was conducted in the Tundra vegetation zone C (CAVM Team 2003) in Adventdalen, on the island of Spitzbergen, Norway (78°63'N, 15°22'W), elevation is between 25 and 50 m above sea level. Adventdalen is a large valley extending from the Isfjord fiord. Only a few geese breed in the valley, however

several thousand pink-footed and barnacle geese graze the area seasonally as they pass through during the spring migration. Caribou/Svalbard reindeer (*Rangifer tarandus (Vrolik)*) are year-round herbivorous residents that graze the area. The study site consists of wet tundra vegetation that is dominated by *Dupontia fisheri (R. Br), Equisetum arvense (L.)*, and to a lesser extent, *Eriophorum scheuchzeri (Hoppe)*, growing from a thick, dominantly *Calliergon richardsonii (Mitt.)*, moss layer. Snowmelt off nearby glaciers and mountains feeds the small streams that maintain the summer-long moisture of the area.

Experimental design

We employed a factorial random block design with two factors: herbivory (three levels) and temperature (two levels). Five blocks with 6 plots, one for each treatment, were constructed in the summer of 2003. Blocks were fenced with flagging tape to prevent caribou from entering and had a system of boardwalks to prevent trampling effects in the wet tundra. Higher temperatures associated with climate change were simulated with open-topped chambers (Marion *et al.* 1997; Hollister and Webber 2000). Placing two captive geese on the $2m^2$ plots for either one hour or five hours at each grazing event produced two levels of herbivory. The herbivory treatments were applied twice in the first and second years of the experiment (2003 and 2004), and once in 2005. The grazing events occurred in early July at the beginning of the growing season (all years), and the second grazing event took place in early August after the peak-growing season

(two first years). If present, OTCs were removed from the plots for approximately 24 hours during the grazing event.

Effect of OTCs

The majority of studies involving OTCs have been conducted on dry tundra. This study was conducted on wet tundra where a thick moss layer extended beyond the saturated soil level. In grazed plots, geese trampled and compacted the moss layer so that it did not extend beyond the soil level and in places standing water remained. OTCs produced a greater warming effect in the saturated soil in the grazed plots (a warming effect detected up to 10 cm below the surface in the plots grazed for 5 hrs) than in ungrazed plots (no soil warming detected), likely as an effect of shading by the moss canopy. OTCs in ungrazed plots produced higher daily maximum temperatures 5 cm above the surface (Appendix A).

Study species

Dupontia fisheri (R. Br.), commonly called Fisher's tundra grass, is a common wet tundra graminoid species with a circumarctic distribution. *Dupontia fisheri* and *Dupontia psilosantha* are classified as separate species in Svalbard (Elven and Elvebakk 1996) although AFLP fingerprinting suggests that all members of the genus be grouped into a single species: *Dupontia fisheri* (Brysting *et al.* 2004). Individual ramets are perennial and take approximately 4 years to mature before flowering (Allessio and Tieszen 1975). Propagation is highly dependant on clonal growth (Brochmann and Steen 1999) through belowground rhizomes.

Mother ramets provide daughter rhizomes with carbon throughout the growing season and connections are maintained between rhizomes until the flowering age is attained (Allesio and Tieszen 1975).

Measurements

We identified ten *D. fisheri* ramets in each plot that were at least in their second summer of growth, but not flowering in 2004. Ramets were marked with a plastic ring and measured on a weekly basis from snowmelt (early June) until near senescence (early September) in the summer of 2004. In 2005, we selected an additional fifteen ramets per plot using the above criteria because the remaining ramets were a year older and thus more likely to flower. These ramets were followed from snow melt (mid June) until mid August (after the peak growing season ended). In both years some ramets were lost due to flowering, or loss of the plastic ring. The length of each leaf was measured from the leaf sheath to the transition from living to dead tissue, and from the leaf sheath to the tip of the leaf. Thus both the living portion of the leaf and its total length are known. Individual leaves were identified by the order in which they emerged on the plant. Measurements were taken within 24 hours before and after the grazing events to ensure that the amounts removed by the geese were known. At the end of August 2005, the aboveground and belowground plant parts were harvested, dried and weighed. The aboveground parts were used to confirm a positive relationship between actual biomass and leaf length measurements (Figure 3-1). The belowground parts were harvested by excavating the rhizome associated with the

ramet. Daughter rhizomes were counted, then removed and the rhizome associated with the ramet was washed, measured, then dried and weighed.

Statistics

Data analyses were conducted in SAS version 8.1 (SAS Institute Inc. 1999). Analyses on cumulative leaf length, number of leaves, leaf length, rhizome masses, and date of maximum living aboveground tissue were analyzed using ANOVAs (Mixed procedure). Block, treatment nested within block, and for the rhizome mass analysis, rhizome length, were treated as random factors. Temperature, grazing and year were treated as fixed factors. In the leaf length analysis, ramet was treated as the subject, an unstructured variance structure was employed and the order of leaf emergence was treated as a random effect. Only the first four leaves were analyzed in this dataset, as this was the maximum number of fully-grown leaves with large sample sizes common to all treatment categories. The fifth, sixth and seventh leaves were not always fully extended, and as some treatment categories had more leaves than others, leaf lengths of these latter leaves was a function of number of leaves in a treatment and not actual leaf length at leaf maturity.

In 2005, the dataset included only new ramets selected in 2005 to make equivalent comparisons with the 2004 set, as the original shoots were a year older than the selection criteria. Ramets that flowered were excluded from the above analyses, as the leaves on flowering ramets are morphologically distinct from those that do not flower; they are substantially shorter and frequently die early on

in the season. Differences among treatments were identified using tests of least square means. The analyses on cumulative leaf length and number of leaves that were used to make comparisons between years were based on the size at the end of August in both years to be comparable, and did not include the final measurement taken in September 2004.

Goose forage selectivity analyses were analyzed using a nested logistic regression of the first grazing events in 2004 and 2005 (Genmode procedure in SAS). The probability of a goose grazing a leaf was modeled using a binary distribution, where the leaf was either grazed or not grazed. Plant was treated as subject and an unstructured variance structure was assumed. The model included leaf length, leaf cohort (at the time of grazing the maximum number of leaves per plant was four in 2004 and three in 2005, so leaf cohort consisted of leaf 1, 2, 3 or 4 in 2004 and leaf 1, 2 or 3 in 2005) and grazing treatment (either 1 hr or 5 hrs). Leaf cohort selectivity indicated preference compared to the first leaf. Whether a ramet was in flower was originally treated in the model, but was not significant and therefore removed from the final model.

Results

Growing season length

Growing season length varied between years. In 2004, snow melted from the plots between 4-14 June. In 2005, the snowmelt period occurred between 19-26 June, an effective difference of 13-16 days since 2004 was a leap year. Growth was delayed in 2005, and the date of peak living biomass was significantly later in

ungrazed controls between the two years (Year $F_{(1,183)}$=42.42, P<0.0001), shifting from the mean date of 28 July 2004 to 4 August 2005, a difference of 8 days (due to leap year). There were no differences in peak biomass date within years between OTCs and ambient plots, or OTC × year interactions (Temperature $F_{(1,9.84)}$=0.02, P=0.8967) (Figure 3 - 2).

Peak living tissue

The maximum living tissue did not differ between years or OTC treatment in the ungrazed plots (Table 3 - 1, Figure 3 - 2). On the day of peak living biomass in both years the values did not differ significantly, however, the day that this occurred was later in 2005 than 2004.

Total aboveground productivity

We used the sum of the maximum leaf lengths attained per ramet at the end of August as an estimate of aboveground productivity per ramet (Figure 3 - 3). OTCs did not affect productivity in either year (Table 3 - 2). In 2004, the second summer of treatment, there were no differences in the productivity of grazed and ungrazed plots. However in the third year of treatment, 2005, ramets in grazed plots were less productive. In addition, ramets in plots grazed for 5 hrs were less productive than ramets in plots grazed for 1 hr. Ramets in the ungrazed plots were only slightly less productive than 2004 (Test of Least Square Means, Year, $F_{(1,545)}$=3.27, P=0.0709).

Leaf production

Number of leaves produced per ramet was significantly affected by grazing-temperature treatment, and by year (Table 3 - 2, Figure 3 - 4). The number of leaves per ramet did not differ between grazing treatments in the ambient plots, however, they did differ in the OTCs. The ramets in the ungrazed OTCs produced the fewest leaves and the ramets in the 5 hr grazing treatments produced the most. In addition, ramets in the ungrazed OTCs and ramets in OTCs that were grazed for 1 hr produced fewer leaves than their counterparts in the ambient plots.

Rhizome mass

Herbivory resulted in reduced rhizome mass ($F_{(2,\ 23.8)}$=11.61, P=0.0003), but temperature had no detectable effect (Figure 3 - 5). Plants in ungrazed plots had almost a third more mass than those in the 5 hrs grazed plots.

Leaf lengths

Maximum leaf lengths varied by treatment and by year (Table 3 - 2, Figure 3 - 6). We did not detect differences in the maximum leaf lengths in the ungrazed plots, either between years or between warming treatments. Ramets in the grazed plots that were not warmed produced shorter leaves than those in ungrazed plots, in both 2004 and 2005. However, leaves in plots that were grazed and warmed were longer than their ambient counterparts in 2004. In 2005, there were no differences between leaf lengths in grazed treatments, although all leaves in

grazed treatments were shorter than ungrazed treatments. The maximum leaf lengths did not differ between ungrazed-warmed and ungrazed-ambient plots.

Goose selectivity

Leaf length, treatment and leaf age affected leaf susceptibility to herbivory. Longer leaves were more likely to be grazed (nested logistic regression, in 2004 estimate=0.0149, Z=2.30, P=0.0212; in 2005 estimate=0.0176, Z=2.09, P=0.0364), leaves in the 5 hr grazing treatment were more likely to be grazed than those in the 1 hr treatment (in 2004 estimate=3.0297, Z=8.01, P<0.0001; in 2005 estimate =-2.0965, Z =-9.69, P<0.0001), and the oldest leaf was less likely to be grazed than the second and third leaves (leaf 1 vs. 2 in 2004 estimate=0.6983, Z=2.84, P=0.0044; in 2005 estimate =-0.9858, Z=-3.37, P=0.0008; leaf 1 vs. 3 in 2004 estimate=1.2526, Z=4.41, P<0.0001, in 2005 estimate=-1.3630, Z=-2.99, P=0.0028; and leaf 1 vs. 4 in 2004 estimate=0.0857, Z=0.18, P=0.8555). Geese selected leaves that were longer and younger.

Discussion

Responses to goose herbivory under ambient temperature

Many, but not all of the responses of *D. fisheri* to goose herbivory in the absence of experimental warming were consistent with our predictions. In the second summer of the experiment, 2004, we did not detect a difference in the cumulative aboveground growth (sum of leaf lengths) among treatments. Grazed plots neither over-compensated, nor under-compensated for tissue lost to herbivory. In

the third summer of treatment, 2005, plants in the grazed plots produced less aboveground growth than those in the ungrazed treatments. We attribute this to a reduction in resources, specifically a reduction of reserves in storage organs. Resources in *D. fisheri* are stored in the over-wintering rhizomes (Beaulieu *et al.* 1996). Upon harvesting in 2005, the rhizomes of *D. fisheri* were significantly lighter per unit length in the grazed treatments than the ungrazed treatments. We interpret this reduction in mass as a consequence of reduced photosynthate accumulation in grazed plots and a reduction of allocation of resources to storage organs in the fall. Grazed plants in 2004 likely produced aboveground growth equally to plants in ungrazed plots, by utilizing belowground reserves. Although we did not harvest rhizomes in other years, it is likely that a reduction in rhizome reserves began in 2003, after the first grazing events and was amplified in subsequent years.

The morphology of ramets in plots subjected to herbivory without warming was consistent with our predictions; ramets subjected to herbivory produced short leaves. Leaves of ramets in ungrazed plots followed a distinctive growth pattern: the first three were ascending in length and thereafter descending. In the absence of herbivory, the first two leaves typically senesced before the end of the growing season, but the third leaf and all subsequent leaves typically survived until the plant as a whole began to senesce in late August. The third and longest leaf of a ramet not subjected to herbivory was typically about 90 mm long when mature, and the fourth and shortest leaf was typically between 50-70 mm long when mature. The third leaf was the longest leaf and investing in its growth

is an efficient strategy for the plant in ungrazed settings because it survives over the longest time period with the warmest temperatures. In the intensely grazed plots, the longest leaf was still the third leaf, however its length was typically around 65 mm, and the fourth leaf was typically around 40-60 mm. Leaves were significantly shorter in the intensely grazed plots and all leaves had similar lengths. Regardless of the mechanism behind such adjustment of leaf morphology to grazing, this short-leaved morphology is likely advantageous to the plant because loss of a leaf of 50 mm is less expensive to the plant than the loss of a leaf twice that length of the same age. Plots that were grazed for 1 hr showed a similar trend in morphology, but leaves were slightly longer, as would be expected in plots experiencing less intensive herbivory. Additionally, in the third summer of treatment, leaves were slightly smaller in the 5 hr treatment than the previous summer.

Responses to warming in the absence of herbivores

The responses of *D. fisheri* to warming in the absence of herbivory were inconsistent with our predictions. We did not detect increases in above- and below- ground productivity, peak living tissue, leaf lengths, number of leaves or onset of senescence in warmed plots compared to controls. Other studies have observed positive effects on plant productivity from warming (e.g. Rustad *et al.* 2001; Kudo and Suzuki 2003), however other resources such as light and nutrients can have greater effects on aboveground biomass than temperature alone (Leadley and Reynolds 1992; Chapin *et al.* 1995; Jonasson *et al.* 1999). The

majority of the biomass of Arctic plants is belowground (Shaver and Chapin 1991), thus a plant can allocate more resources to storage organs in favourable conditions. For this reason we might expect rhizomes to increase in mass. However we did not detect differences. Belowground responses are difficult to measure, and our methods were not sensitive to subtle differences in productivity. Increases in leaf length as a response to warming have been observed in other species (e.g. Stenström and Jónsdóttir 1997; Hollister *et al.* 2005a; Marchand *et al.* 2005), however we did not detect this response in *D. fisheri*. Hollister *et al.* (2005a), did not detect an increase in *D. fisheri* leaf length in response to OTC treatment either.

Studies that have achieved major responses to warming, such as the Toolik Lake study, increased temperatures substantially with closed greenhouses where maximum air temperatures were increased by 10°C, and soil surface temperatures were increased by 5°C (Chapin *et al.* 1995). In our study, warming achieved by OTCs may have been insufficient to elicit a positive response from *D. fisheri*. Alternately, we did observe, contrary to our predictions, a significant decrease in the number of leaves produced in warmed plots. Although this decrease was slight (0.3 leaves fewer), it could indicate a cost to *D. fisheri* associated with warming. Hollister *et al.* (2005a) documented a delay in the phenological development *D. fisheri* in response to warming in Alaska. Within the range of warming we achieved, we did not detect a positive response in *D. fisheri* to increased temperatures in the absence of herbivory.

Responses to goose herbivory and warming

We predicted that warming would mitigate the response of plants to herbivory. While there were no differences in productivity, we did observe a temporal shift in the morphological response to herbivory in warmed plants. Ramets, in the absence of warming, produced the short-leaved morphology described above, in both the second and third summers of herbivory treatment. Ramets that were both warmed and grazed produced the long-leaved morphology in the second summer of treatment and the short-leaved morphology in the third summer of treatment. In the second summer of treatment, the third leaf of the 5 hr warming treatment was about 80 mm in length, compared to 90 mm in ungrazed plants and 65 mm in the 5 hr ambient plots. By the third summer of treatment, leaf lengths did not differ between the 5 hr grazed treatments, irrespective of warming. Leaves were shortest in the plots that were grazed for 5 hrs, however the same trends exist in the plots grazed for 1 hr. Intensity of herbivory did not alter the direction of the response to warming, but only its strength.

These responses to herbivory and warming illustrate a trade-off for the plant between the risk of herbivory and the costs associated with herbivory tolerant morphologies. We showed geese are highly selective herbivores, selecting younger and longer leaves. In the presence of selective herbivores, long leaves are disadvantageous as they are more likely to become grazed. In addition, the loss of a long leaf is more costly to the plant than the loss of a short leaf of the same age, as more tissue is removed by the herbivore. However, short leaves are also costly to the ramet because they have smaller surface areas that are less

efficient at accumulating photosynthate than large surface areas. Additionally more time and resources are required to produce many short leaves compared to a few long leaves. Warmer temperatures of only a few degrees can result in considerably higher rates of photosynthesis (Woodward 1993). Thus the short-leaved morphology was probably costly to the plant in terms of lost photsynthate accumulation. Thus the strategy of a plant subjected to herbivory may take both the potential costs and potential benefits associated with that strategy into account. The delayed response to herbivory in warmed plots may be an indication of the costs associated with producing short leaves: a reduced ability to exploit warm temperatures and accumulate resources. However the shift to a short-leaved, herbivore-tolerating morphology in the third summer of treatment may be indicative of the costs associated with the long-leaved morphologies in the presence of herbivores.

Ability of D. fisheri *to respond to climate change*

Although a response to warmer temperatures was observed in grazed treatments the lack of response to warming in ungrazed treatments stands out. This lack of response to warming in the absence of herbivores could be due to reduced heating by OTCs in un-trampled plots, or it may be because *D. fisheri* does not have phenotypes capable of exploiting warmer temperatures. *D. fisheri* has a circumarctic distribution and was likely the product of an intergeneric hybridization event between at least one Arctic species, *Arctophila fulva*

(Brysting *et al.* 2004). This Arctic origin could preclude it from phenotypes capable of exploiting warm conditions.

Climate change is predicted to alter growing season lengths, as well as increase temperatures (ACIA 2005). The onset of the growing season in the last two years of our experiment differed by about two weeks and this allowed us to observe the response of *D. fisheri* to variation in growing season length. Although the growing season occurred two weeks later in 2005 than 2004, the total cumulative productivity in ungrazed treatments was not significantly lower in 2005. Additionally, the peak living biomass attained did not differ significantly between years in ungrazed plots, however the dates that these occurred on were significantly later in the season in 2005. Effectively, the entire growing season in 2004 occurred earlier than in 2005, from the onset until senescence. *D. fisheri* is a cold adapted plant and is robust to a certain degree of variability to changes in growing season length, however it does not appear to be able to take great advantage of longer growing seasons, as it senesces earlier. These inabilities to exploit warmer temperatures and longer growing seasons may indicate it is a species that will be sensitive to competition from species that can better exploit these conditions.

Conclusion

In this study, *Dupontia fisheri* responded to both temperature and herbivory, however warming was subordinate to herbivory after three years of intensive herbivory. After three years of treatments, plants that were warmed and grazed

resembled plants that were grazed without warming, in both morphology and productivity. We observed significant costs of grazing on plant productivity, however, we also observed costs associated with herbivory-tolerant morphologies. Our herbivory treatments occurred in intensive periods over three years, and may be more intensive than many Arctic plants experience. In natural environments where plants will face occasional herbivory and warming, the strategies selected may reflect the new cost/benefits associated with different climatic conditions, as they appeared to in the second year of treatment in our experiment. However the ability of a species to respond to warmer conditions is restricted to the range of phenotypes it can produce. *Dupontia fisheri* is a species adapted to Arctic conditions and may be unable to take advantage of warmer climatic conditions or longer growing seasons. This can make it susceptible to increased competition from species whose competitive ability is enhanced by climate change.

We have shown that warmer temperatures can have little to no effect on some species growing in the absence of herbivores, however when stressed by herbivores, responses to warming become apparent. This suggests that studies that ignore herbivores can be underestimating the potential responses of plants to climate change. In the Arctic, vertebrate herbivores remove a substantial portion of primary productivity and consequently have a significant influence on the dynamics of the vegetation (Oksanen *et al.* 1981; Jefferies *et al.* 1992). To make accurate predictions surrounding the effects of climate change in the next century, it will be necessary to consider how trophic interactions such as herbivory affect vegetation.

Table 3-1: General linear tests of mixed models of peak living tissue, cumulative leaf length, number of leaves and leaf lengths. Tests of simple effects were conducted on significant interactions to identify at which levels of treatment produced significance.

Subject	Model term		$F_{(Numdf,Dendf)}$	P
	Tests of Simple Effects			
Peak living tissue (mm)	**Temperature**		$0.03_{(1,4.78)}$	0.8593
	Year		$1.59_{(1,184)}$	0.2091
	Temperature × Year		$0.42_{(1,183)}$	0.5178
Cumulative leaf length	**Temperature**		$0.00_{(1,25.1)}$	0.9889
	Graze		**$9.28_{(2,25)}$**	**0.0010**
	Year		**$47.27_{(1,546)}$**	**<0.0001**
	Temperature × Year		$1.41_{(1,546)}$	0.2355
	Temperature × Graze		$1.55_{(2,25)}$	0.2319
	Graze × Year		**$3.83_{(2,546)}$**	**0.0223**
	Year	*Ungrazed*	$3.27_{(1,545)}$	0.0709
		1 hr graze	**$18.96_{(1,550)}$**	**<0.0001**
		5 hrs graze	**$33.97_{(1,543)}$**	**<0.0001**
	Graze	*2004*	$1.51_{(2,67.3)}$	0.2283
		2005	**$13.74_{(2,52.9)}$**	**<0.0001**
	Temperature × Graze × Year		$0.88_{(2,546)}$	0.4152
Number of leaves	**Temperature**		**$4.50_{(1,25.6)}$**	**0.0437**
	Graze		**$5.47_{(2,25.5)}$**	**0.0106**
	Year		**$40.07_{(1,546)}$**	**<0.0001**
	Temperature × Year		$0.66_{(1,547)}$	0.4164
	Temperature × Graze		**$5.40_{(2,25.5)}$**	**0.0111**
	Temperature	*Ungrazed*	**$7.84_{(1,26.7)}$**	**0.0094**
		1 hr graze	**$4.96_{(1,26.7)}$**	**0.0346**
		5 hrs graze	$2.08_{(1,23.3)}$	0.1629
	Graze	*Ambient*	$0.65_{(2,26.7)}$	0.5295
		OTC	**$10.35_{(2,24.3)}$**	**0.0006**
	Graze × Year		$0.69_{(2,547)}$	0.5011
	Temperature × Graze × Year		$0.66_{(2,547)}$	0.5178

Table 3-1: continued.

Subject	Model term		$F_{(Numdf,Dendf)}$	P
	Tests of Simple Effects			
Leaf length	**Temperature**		$2.14_{(1,24.7)}$	0.1557
	Graze		$\mathbf{18.32}_{(2,24.7)}$	**<0.0001**
	Year		$\mathbf{28.23}_{(1,478)}$	**<0.0001**
	Temperature × Graze		$0.22_{(2,24.7)}$	0.8052
	Graze × Year		$\mathbf{2.85}_{(2,478)}$	**0.0053**
	Year × Temperature		$\mathbf{3.83}_{(1,478)}$	**0.0510**
	Temperature × Graze × Year		$\mathbf{2.85}_{(2,478)}$	**0.0586**
	Temperature × Year	*Ungrazed*	$0.32_{(3,122)}$	0.8110
		1 hr graze	$\mathbf{5.55}_{(3,125)}$	**0.0013**
		5 hrs graze	$\mathbf{11.19}_{(3,116)}$	**<0.0001**
	Year	*Ambient × Ungrazed*	$0.70_{(1,473)}$	0.4048
		Ambient × 1 hr graze	$2.68_{(1,474)}$	0.1021
		Ambient × 5 hrs graze	$2.48_{(1,479)}$	0.1157
		OTC × Ungrazed	$0.02_{(1,488)}$	0.9013
		OTC × 1 hr graze	$\mathbf{13.67}_{(1,486)}$	**0.0002**
		OTC × 5 hrs graze	$\mathbf{29.61}_{(1,468)}$	**<0.0001**
	Temperature	*2004 × Ungrazed*	$0.00_{(1,55.5)}$	0.9987
		2004 × 1 hr graze	$1.86_{(1,58)}$	0.1775
		2004 × 5 hrs graze	$\mathbf{7.37}_{(1,51.5)}$	**0.0090**
		2005 × Ungrazed	$0.63_{(1,54)}$	0.4297
		2005 × 1 hr graze	$0.08_{(1,56.6)}$	0.7824
		2005 × 5 hrs graze	$0.18_{(1,59.4)}$	0.6747

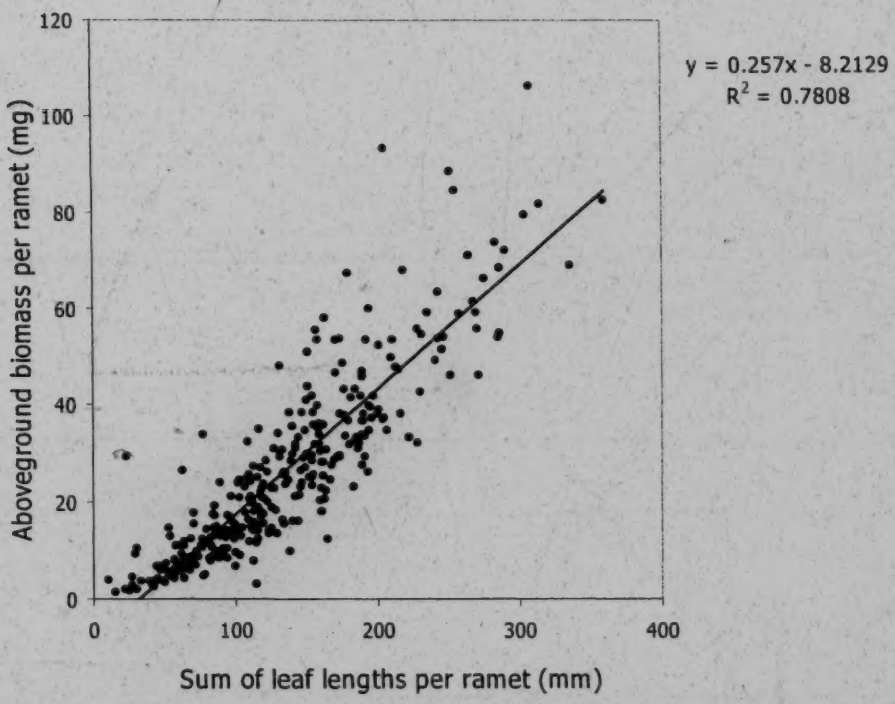

Figure 3-1: Relationship between cumulative leaf lengths and biomass (mg) at the end of August 2005.

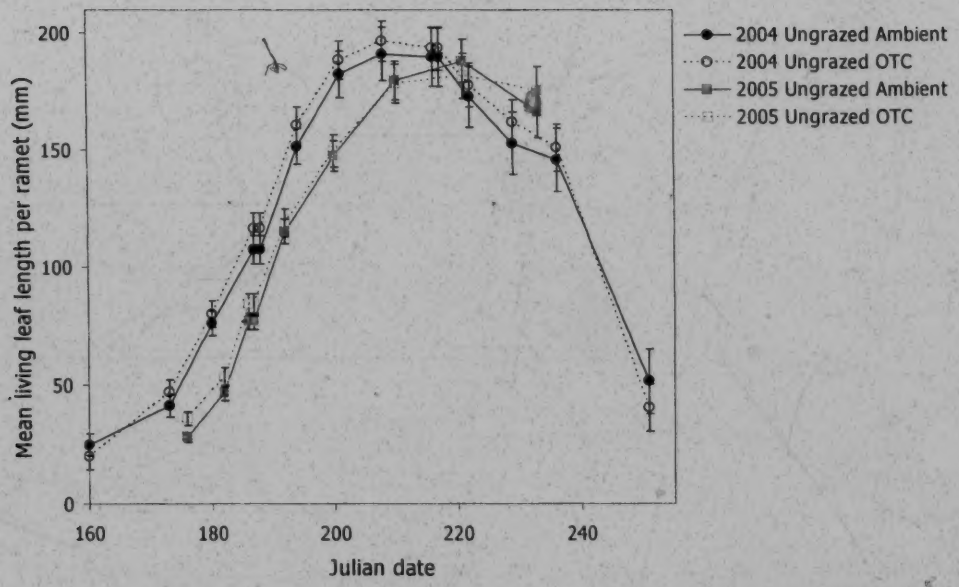

Figure 3-2: Living tissue per ramet in 2004 and 2005 in ungrazed treatments. Onset of growing season occurred later in 2005 than 2004. Peak living tissue did not differ between years or temperature treatments, but the date of maximum tissue occurred significantly later in 2005. Error bars represent 1 standard error.

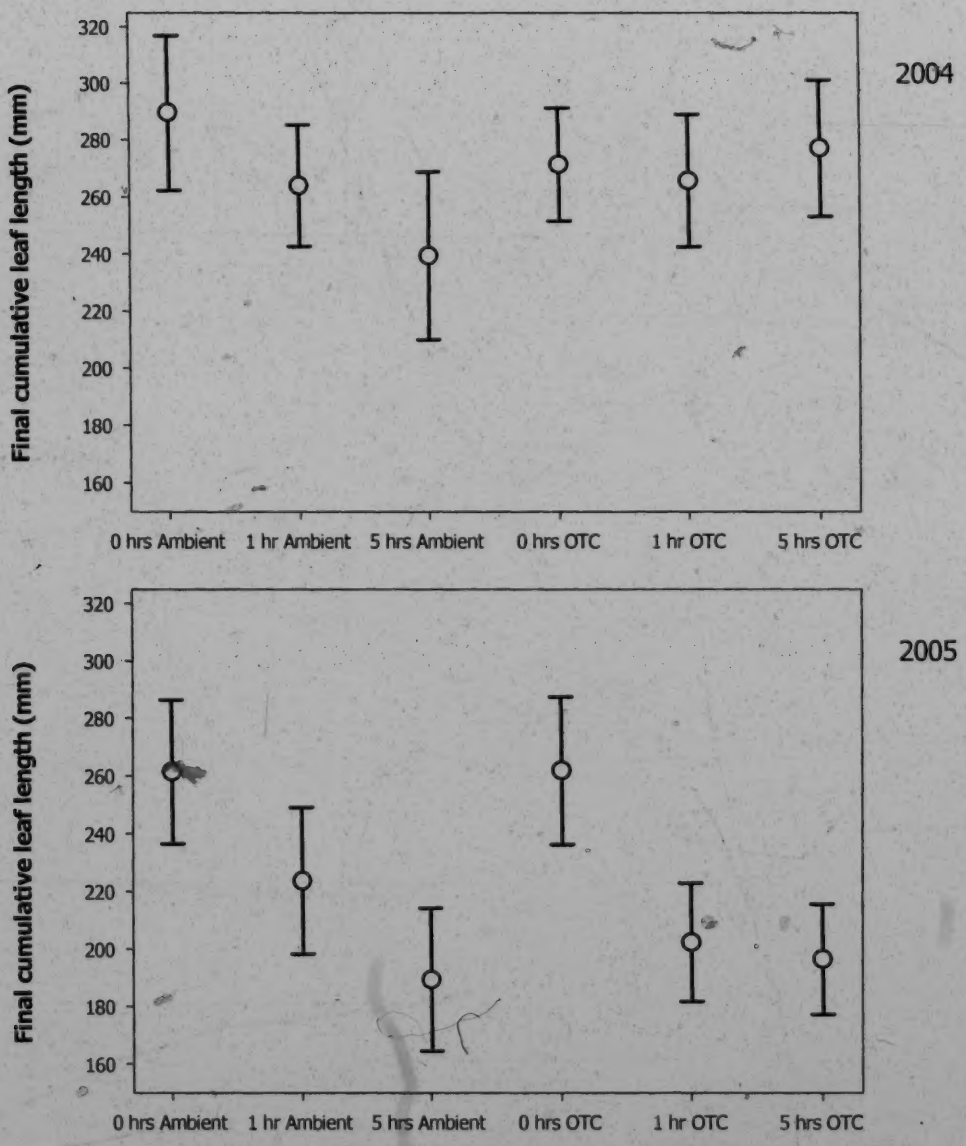

Figure 3-3: Total cumulative tissue accumulated per ramet at the end of the 2004 and 2005 growing seasons (mean +/- CI). Cumulative tissue at the end of the growing season did not differ among treatments in 2004 but was significantly lower in the treatments that were grazed in 2005.

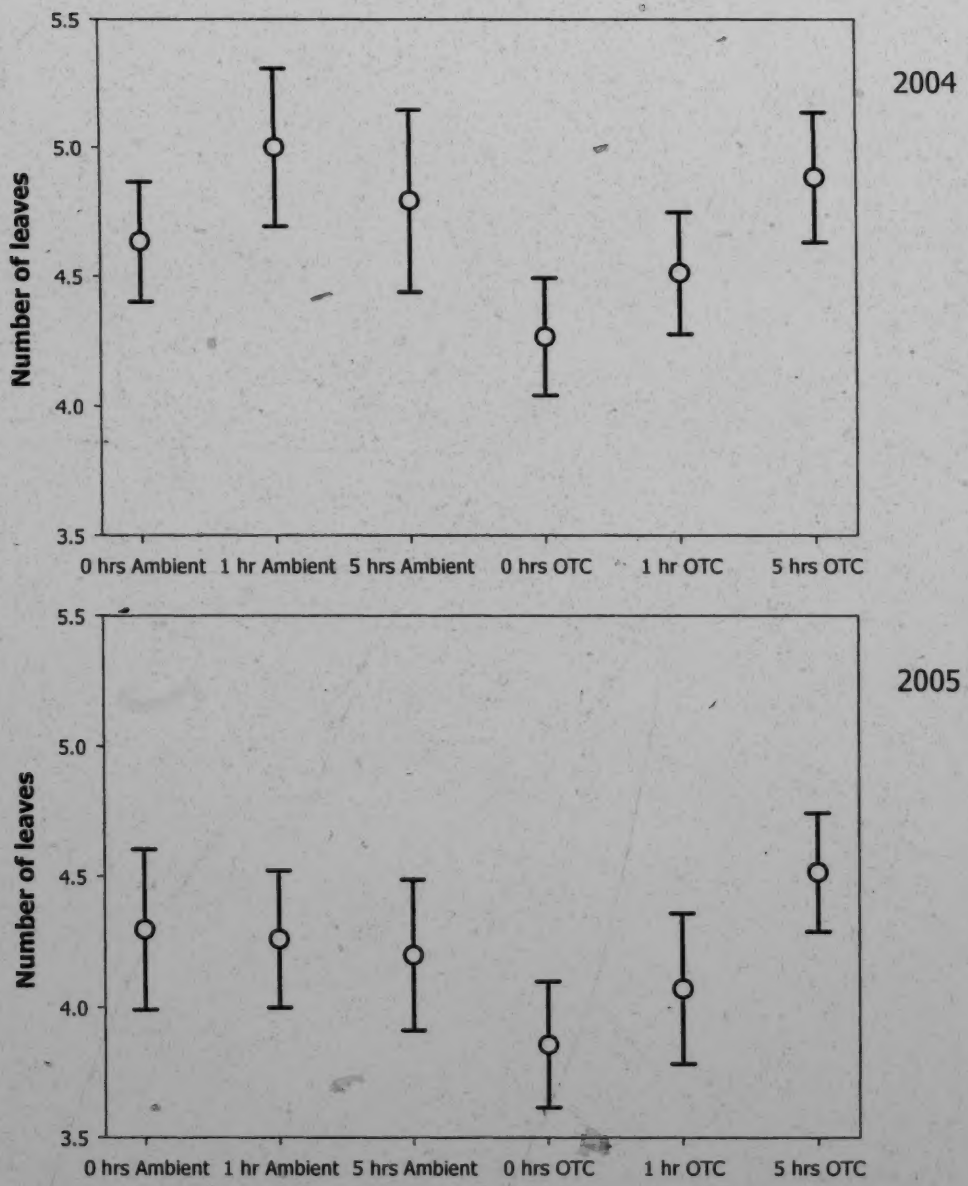

Figure 3-4: Number of leaves produced per ramet for each treatment at the end of August in 2004 and 2005 (Mean +/- CI).

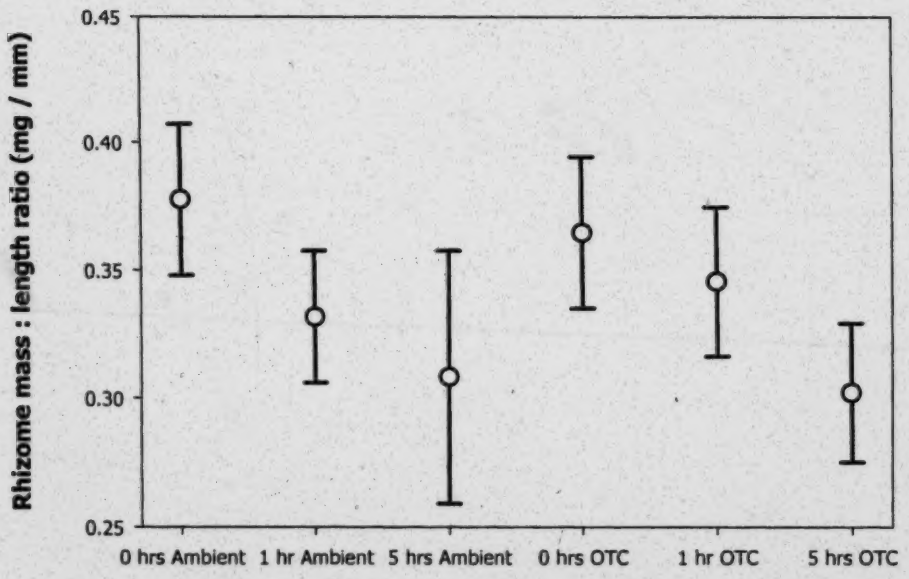

Figure 3-5: Rhizome mass : length ratio (mg/mm) mean +/- 95% CI; grazing significantly reduced the mass of rhizomes when length was controlled.

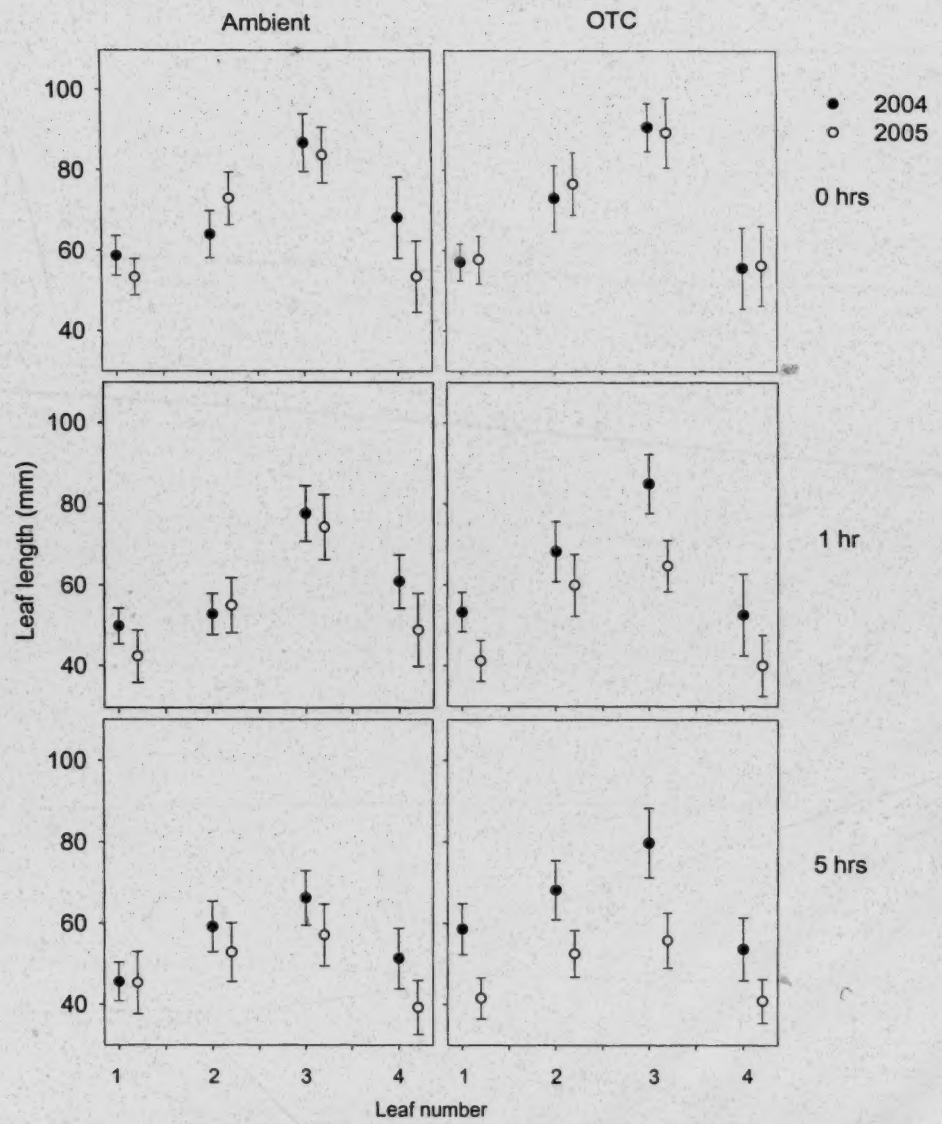

Figure 3-6: First four leaf lengths of ramets in both 2004 and 2005 (mean+/- CI). Ramets produced longer leaves in 2004 in the grazed treatments that were warmed than those that were not warmed. There was no difference between the leaf lengths of leaves from ambient plots.

Literature Cited

ACIA (2005) Arctic Climate Impact Assessment. Cambridge University Press, Cambridge.

Allessio ML, Tieszen LL (1975) Patterns of carbon allocation in an Arctic tundra grass, *Dupontia fischeri* (Gramineae), at Barrow, Alaska. *American Journal of Botany*, **62**, 797-807.

Arft AM, Walker MD, Gurevitch J, Alatalo JM, Bret-Harte MS, Dale M, Diemer M, Gugerli F, Henry GHR, Jones MH, Hollister RD, Jónsdóttir IS, Laine K, Levesque E, Marion GM, Molau U, Molgaard P, Nordenhall U, Raszhivin V, Robinson CH, Starr G, Stenstrom A, Stenstrom M, Totland O, Turner PL, Walker LJ, Webber PJ, Welker JM, Wookey PA (1999) Responses of tundra plants to experimental warming: Meta-analysis of the international tundra experiment. *Ecological Monographs*, **69**, 491-511.

Bazely DR, Jefferies RL (1989) Leaf and shoot demography of an Arctic stoloniferous grass, *Puccinellia phryganodes*, in response to grazing. *Journal of Ecology*, **77**, 811-822.

Beaulieu J, Gauthier G, Rochefort L (1996) The growth response of graminoid plants to goose grazing in a High Arctic environment. *Journal of Ecology*, **84**, 905-914.

Brochmann C, Steen SW (1999) Sex and genes in the flora of Svalbard – implications for conservation biology and climate change. *Norske*

Videnskapelig.-Akademi. I. Matematisk Naturvitenskapelig Klasse, Ny serie, **38**, 33-72.

Brysting AK, Fay MF, Leitch IJ, Aiken SG (2004) One or more species in the Arctic grass genus *Dupontia*? - a contribution to the Panarctic Flora project. *Taxon*, **53**, 365-382.

Callaghan TV, Bjorn LO, Chernov Y, Chapin T, Christensen TR, Huntley B, Ims RA, Johansson M, Jolly D, Jonasson S, Matveyeva N, Panikov N, Oechel W, Shaver G, Henttonen H (2004) Effects on the structure of Arctic ecosystems in the short- and long-term perspectives. *Ambio*, **33**, 436-447.

Cargill SM, Jefferies RL (1984a) Nutrient limitation of primary production in a Sub-Arctic salt-marsh. *Journal of Applied Ecology*, **21**, 657-668.

Cargill SM, Jefferies RL (1984b) The effects of grazing by lesser Snow Geese on the vegetation of a Sub-Arctic salt-marsh. *Journal of Applied Ecology*, **21**, 669-686.

CAVM Team (2003) Circumpolar Arctic Vegetation Map. Scale 1:7,500,000. Conservation of Arctic Flora and Fauna (CAFF) Map No. 1. U.S. Fish and Wildlife Service, Anchorage, Alaska

Chapin FS, Shaver GR, Giblin AE, Nadelhoffer KJ, Laundre JA (1995) Responses of Arctic tundra to experimental and observed changes in climate. *Ecology*, **76**, 694-711.

Elven R, Elvebakk A (1996) Part 1. Vascular plants. In: A *catalogue of Svalbard plants, fungi, algae and cyanobacteria* (eds Elvebakk A Prestrud P) Oslo, Norway, Norsk Polarinstitutt Skrifter.

Gauthier G, Hughes RJ, Reed A, Beaulieu J, Rochefort L (1995) Effect of grazing by Greater Snow Geese on the production of graminoids at an Arctic site (Bylot Island, NWT, Canada). *Journal of Ecology*, **83**, 653-664.

Henry GHR, Molau U (1997) Tundra plants and climate change: the International Tundra Experiment (ITEX). *Global Change Biology*, **3**, 1-9.

Hik DS, Sadul HA, Jefferies RL (1991) Effects of the timing of multiple grazings by geese on net aboveground primary production of swards of *Puccinellia phryganodes*. *Journal of Ecology*, **79**, 715-730.

Hollister RD, Webber PJ (2000) Biotic validation of small open-top chambers in a tundra ecosystem. *Global Change Biology*, **6**, 835-842.

Hollister RD, Webber PJ, Bay C (2005a) Plant response to temperature in Northern Alaska: Implications for predicting vegetation change. *Ecology*, **86**, 1562-1570.

Hollister RD, Webber PJ, Tweedie CE (2005b) The response of Alaskan Arctic tundra to experimental warming: differences between short- and long-term responses. *Global Change Biology*, **11**, 525-536.

Houghton J (2001) The science of global warming. *Interdisciplinary Science Reviews*, **26**, 247-257.

IPCC Report (2001) IPCC Third Assessment Report – Climate Change 2001.

Jefferies RL, Svobboda J, Henry G, Raillard M, Ruess R (1992) Tundra grazing systems and climatic change. In: *Arctic Physiological Processes in a Changing Climate.* (eds Chapin T, Jeffries D, Reynolds J, Shaver G, Svoboda J) pp. 391-412. Academic Press, San Diego.

Jonasson S, Michelsen A, Schmidt IK, Nielsen EV (1999) Responses in microbes and plants to changed temperature, nutrient, and light regimes in the Arctic. *Ecology*, **80**, 1828-1843.

Kotanen P, Jefferies RL (1987) The leaf and shoot demography of grazed and ungrazed plants of *Carex subspathacea*. *Journal of Ecology*, **75**, 961-975.

Kotanen PM, Jefferies RL (1997) Long-term destruction of sub-arctic wetland vegetation by lesser snow geese. *Ecoscience*, **4**, 179-182.

Kudo G, Suzuki S (2003) Warming effects on growth, production, and vegetation structure of alpine shrubs; a five-year experiment in northern Japan. *Oecologia*, **135**, 280-287.

Leadley PW, Reynolds JF (1992) Long-term response of an Arctic sedge to climate change – a simulation study. *Ecological Applications*, **2**, 323-340.

Marchand FL, Mertens S, Kockelbergh F, Beyens L, Nijs I (2005) Performance of High Arctic tundra plants improved during but deteriorated after exposure to a simulated extreme temperature event. *Global Change Biology*, **11**, 2078-2089.

Marion GM, Henry GHR, Freckman DW, Johnstone J, Jones G, Jones MH, Levesque E, Molau U, Molgaard P, Parsons AN, Svoboda J, Virginia RA (1997) Open-top designs for manipulating field temperature in high-latitude ecosystems. *Global Change Biology*, **3**, 20-32.

Marion GM, Miller PC, Kummerow J, Oechel WC (1982) Competition for nitrogen in a tussock tundra ecosystem. *Plant and Soil*, **6**, 317-327

McIntire EJB, Hik DS (2002) Grazing history versus current grazing: leaf demography and compensatory growth of three alpine plants in response to a native herbivore (*Ochotona collaris*). *Journal of Ecology*, **90**, 348-359.

McNaughton SJ (1984) Grazing lawns - animals in herds, plant form, and coevolution. *American Naturalist*, **124**, 863-886.

Neilson RP, Pitelka LF, Solomon AM, Nathan R, Midgley GF, Fragoso JMV, Lischke H, Thomspon K (2005) Forecasting regional to global plant migration in response to climate change. *BioScience*, **55**, 749-759.

Oechel WC, Billings WD (1992) Effects of Global Change on the Carbon Balance of Arctic Plants and Ecosystems. In: *Arctic Physiological*

Processes in a Changing Climate. (eds Chapin T, Jeffries D, Reynolds J, Shaver G, Svoboda J) pp 139-168. Academic Press, San Diego

Oechel WC, Hastings SJ, Vourlitis G, Jenkins M, Riechers G, Grulke N (1993) Recent change of Arctic tundra ecosystems from a net carbon-dioxide sink to a source. *Nature*, **361**, 520-523.

Oksanen L, Fretwell SD, Arruda J, Niemela P (1981) Exploitation ecosystems in gradients of primary productivity. *American Naturalist*, **118**, 240-261.

Olofsson J (2006) Plant diversity and resilience to reindeer grazing. *Arctic Antarctic and Alpine Research*, **38**, 131-135.

Olofsson J, Kitti H, Rautiainen P, Stark S, Oksanen L (2001) Effects of summer grazing by reindeer on composition of vegetation, productivity and nitrogen cycling. *Ecography*, **24**, 13-24.

Richardson SJ, Hartley SE, Press MC (2000) Climate warming experiments: are tents a potential barrier to interpretation? *Ecological Entomology*, **25**, 367-370.

Rustad LE, Campbell JL, Marion GM, Norby RJ, Mitchell MJ, Hartley AE, Corneliessen JHC, Gurevitch KJ (2001) A meta-analysis of the response of soil respiration, net nitrogen mineralization, and aboveground plant growth to experimental ecosystem warming. *Oecologia*, **126**, 543-562.

SAS Institute Inc. (1999) Cary, NC, USA

Shaver GR, Billings WD, Chapin FS, Giblin AE, Nadelhoffer KJ, Oechel WC, Rastetter EB (1992) Global change and the carbon balance of Arctic ecosystems. *Bioscience*, **42**, 433-441.

Shaver GR, Chapin FS (1991) Biomass relationships and element cycling in contrasting Arctic vegetation types. *Ecological Monographs*, **61**, 89-96.

Stenstrom A, Jónsdóttir IS (1997) Responses of the clonal sedge, *Carex bigelowii*, to two seasons of simulated climate change. *Global Change Biology*, **3**, 89-96.

Suzuki S, Kudo G (2000) Responses of alpine shrubs to simulated environmental change during three years in the mid-latitude mountain, Northern Japan. *Ecography*, **23**, 553-564.

Van der Wal R, Van Lieshout SMJ, Loonen MJJE (2001) Herbivore impact on moss depth, soil temperature and Arctic plant growth. *Polar Biology*, **24**, 29-32.

Van der Wal R, Bardgett RD, Harrison KA, Stien A (2004) Vertebrate herbivores and ecosystem control: cascading effects of faeces on tundra ecosystems. *Ecography*, **27**, 242-252.

Van Wijk MT, Williams M, Laundre JA, Shaver GR (2003) Interannual variability of plant phenology in tussock tundra: modelling interactions of plant productivity, plant phenology, snowmelt and soil thaw. *Global Change Biology*, **9**, 743-758.

Van Wijk MT, Clemmensen KE, Shaver GR, Williams M, Callaghan TV, Chapin FS, Cornelissen JHC, Gough L, Hobbie SE, Jonasson S, Lee SA, Michelsen A, Press MC, Richardson SJ, Rueth H (2004) Long-term ecosystem level experiments at Toolik Lake, Alaska, and at Abisko, Northern Sweden: generalizations and differences in ecosystem and plant type responses to global change. *Global Change Biology*, **10**, 105-123.

Wahren CHA, Walker MD, Bret-Harte MS (2005) Vegetation responses in Alaskan Arctic tundra after 8 years of a summer warming and winter snow manipulation experiment. *Global Change Biology*, **11**, 537-552.

Woodward FI (1993) Leaf responses to the environment and extrapolation to larger scales. In: *Vegetation Dynamics and Global Change* (eds Solomon AM, Shugart HH) pp. 71-100. Chapman and Hall.

CHAPTER 4

GENERAL DISCUSSION

Herbivory and warming

This thesis reported on the responses of two High Arctic wet-tundra plant species to goose herbivory and simulated climate change warming. Herbivory has major effects on vegetation structure, species composition, and productivity in most ecosystems on Earth (Fretwell 1977; Oksanen *et al.* 1981; McNaughton 1983; Milchunas and Lauenroth 1993; Srivastava and Jefferies 1996; Olofsson 2006). However, few studies have incorporated herbivores into climate change studies of vegetation (e.g. Arft *et al.* 1999). Some notable exceptions include Veteli *et al.* (2002); Karlsson *et al.* (2004); Roy *et al.* (2004); Klein *et al.* (2005); Zvereva and Kozlov (2006); and Flynn *et al.* (2006).

The two species I examined responded to warming and herbivory, however these responses were expressed in different ways. The response of *Equisetum arvense* was an intermediate expression of the responses to each factor alone (Chapter 2). Warming accelerated growth and caused the production of longer branches early in the spring, while herbivory impeded growth and reduced rhizome reserves. When combined, an intermediate growth response was elicited, where the growth rate was similar to that of controls, however rhizome reserves became depleted and ramets produced longer branch lengths.

The response of *Dupontia fisheri* was not characteristic of the intermediate blending of responses observed for *E. arvense*, but rather demonstrated a shift in

response time to herbivory (Chapter 3). Grazing in some graminoid species causes the plant to produce a short-leaved morphology (e.g. McNaughton 1984; McIntire and Hik 2002), which was observed in the second year of treatment in the ambient plots. Warming, on the other hand, causes a long-leaved morphology in many graminoid species (Hollister *et al.* 2005; Marchand *et al.* 2005; Stenström and Jónsdóttir 1997). We did not observe this response in the ungrazed ramets, however in the second year of treatment, ramets that were warmed and grazed produced longer leaves than those that were not warmed. Warming delayed the induction of the short-leaved morphology by one year. In the third year of treatment, all grazed plots produced the short-leaved morphology and the plants that were both warmed and grazed resembled the strictly grazed plants. The responses of these two species indicate warming and herbivory are both likely to have important roles in determining plant productivity and morphology in a future warmer climate.

Abilities of species to respond to climate change

Equisetum arvense and *Dupontia fisheri* have very different origins and histories. *E. arvense* is a widely distributed species, from an ancient lineage, growing from temperate regions to the Arctic (Gifford 1989; Cody 1996). *D. fisheri*, by comparison, is an arctic adapted species, originating from an inter-generic hybridization event where at least one of the parent species was restricted to the Arctic (Brysting *et al.* 2004). *E. arvense* genets occurring in the Arctic could have a wider range of phenotypes at their disposal to exploit a greater range of warmer

climatic conditions than species with more restricted distributions. We did not detect any positive effects of warming on ungrazed plants of *D. fisheri* and this species appears to have little capacity to exploit climate warming conditions as imposed in this experiment in the absence of herbivores. Indeed, a slight cost in terms of the number of leaves produced per ramet was observed. Hollister *et al.* (2005) observed delayed phenological development in response to warming in *D. fisheri* in Alaska. These results indicate that *D. fisheri* could be adapted to cold climate conditions such that it is unable to respond to warmer conditions. This suggests that it could be susceptible to competition from species that can exploit warmer conditions, such as *E. arvense.*

Grasslands and shrublands

Zimov *et al.* (1995) claim the extinction of mega-herbivores caused the shift from grass-dominated tundra to moss dominated tundra at the end of the Pleistocene. Arctic ecosystems stil l have many herbivores such as caribou, muskoxen, voles, lemmings, and migratory waterfowl, however few studies have incorporated them in their climate change studies. Long-term (> 8 years) studies of tundra responses to warming indicate that warming will promote shrubs and possibly cause declines in graminoids and forbs (Chapin *et al.* 1995; Wahren *et al.* 2005; Walker *et al.* 2006). However, strong herbivory pressures promote graminoids and reduce shrubs in these same biomes (Eskelinen and Oksanen 2006; Olofsson 2006). It is possible that the dominant growth response of shrubs in these studies may be partially due to the exclusion of herbivores. Thus studies that examine the

effects of warmer temperatures from climate change without incorporating herbivores may not be providing accurate models of ecosystem responses to climate change. More studies investigating warming with herbivores are needed to determine whether the extent of the responses to warming that occur in the absence of herbivores also occur in their presence.

Mis-timings between plants and herbivores

Many Arctic and Northern herbivores are migratory or seasonal, and plant species are exploited at specific times of the year. When vegetation responds to climatic cues that herbivores do not respond to, mis-timings between phenological states of vegetation and migratory herbivores could occur (Visser and Both 2005). This can have detrimental effects on the herbivores and/or vegetation. In Northern Canada, snow geese cause the transition from productive salt marshes to hypersaline conditions by grubbing belowground plant parts (Srivastava and Jefferies 1996). This occurs predominantly when geese arrive before aboveground vegetation has begun growing (Jefferies *et al.* 2004). The cues that trigger migration are not fully understood and climate change could amplify the number of mis-timings between migratory herbivores, and even seasonal herbivores, and the vegetation.

Too many variables?

By definition ecosystems are complicated and any model representing an ecosystem can be criticized for being too simple. Global change encompasses

many ecosystems, ecological processes, and species over an enormous geographical and temporal scale (IPCC 2001). Even examining the responses of Arctic plants to climate change in the short term, a very small ecosystem component, is an enormous and complex undertaking. In this thesis I take the position that herbivory is a critical factor driving plant responses, but there are also many other important drivers that will interact with warmer temperatures and with each other to varying degrees. Other known relevant abiotic factors impacting arctic plant growth are rising levels of CO_2, changes in cloud cover, precipitation, growing season length, and changes in nutrient biogeochemical cycles (Chapin *et al.* 1995; Galen and Stanton 1995; Malanson and Cairns 1995; Drake *et al.* 1997; Griffin *et al.* 2001; Bates *et al.* 2006). A number of biotic factors could also be important such as the migrations of species from lower latitudes resulting in new, intra-trophic interactions such as competition, facilitation as well as inter-trophic interactions from predators, detritivores and herbivores (Convey *et al.* 2002; Heegaard and Vandvik 2004; Ims and Fuglei 2005; Klanderud 2005; Neilson *et al.* 2005; Dollery *et al.* 2006). The actual responses of arctic plants to warming will likely depend on locality and microclimatic conditions, and will encompass some, or all of these factors, or others that have not yet been identified. In this thesis, I reported on the effects of warming and herbivory only, although these other components could be vital.

Scale

This study was conducted in a single site in Adventdalen, Svalbard. The warming was achieved with OTCs and herbivory was experimental and controlled. Geese in the wild do not remain on a 2 x 2 m area for 1 or 5 hrs twice during the summer, leaving it untouched the remaining weeks. These issues make scaling-up to the entire Arctic from this single locality and two plant species problematic. However herbivory has not received much attention in a climate change context and my goal was to investigate whether warming and herbivory could act synergistically to affect plants. The responses I observed support this view and indicate that herbivory and warming have the potential to interact and produce different plant responses than would occur without this synergy.

FRAGILE context

This thesis was conducted within the FRAGILE framework (Chapter 1). Other members of FRAGILE studied changes in species composition, nutrient cycling, and the responses of the geese to the herbivory and OTC treatments. My work provided the detailed responses of two plant species during the final two years of the three year study. Three years is a short period of time for ecosystem-level changes to occur in response to mild treatments. Small changes that over time may eventual result in ecosystem-level effects are more likely to be observed as plant-level responses to treatments over a short temporal period.

Future research

In line with these findings, future work should examine the responses of species assemblages to warming and herbivory in a wider range of sites with a wider range of herbivores. Although the effects of invertebrate herbivores is not overly important to vascular plants in Svalbard at present, warming will likely increase their numbers, and they could have a more important role in future climates. In addition, other parts of the Arctic are more significantly affected by invertebrate herbivores, thus the role of invertebrates should not be ignored. In this thesis I focused on the responses of plants to herbivory and warming, however I did not integrate changes in vegetation to herbivore responses. Future studies should also include the response of herbivores to changes in vegetation productivity, quality and species composition.

Literature Cited

Arft AM, Walker MD, Gurevitch J, Alatalo JM, Bret-Harte MS, Dale M, Diemer M, Gugerli F, Henry GHR, Jones MH, Hollister RD, Jónsdóttir IS, Laine K, Levesque E, Marion GM, Molau U, Molgaard P, Nordenhall U, Raszhivin V, Robinson CH, Starr G, Stenstrom A, Stenstrom M, Totland O, Turner PL, Walker LJ, Webber PJ, Welker JM, Wookey PA (1999) Responses of tundra plants to experimental warming: Meta-analysis of the international tundra experiment. *Ecological Monographs*, **69**, 491-511.

Bates JD, Svejcar T, Miller RF, Angell RA (2006) The effects of precipitation timing on sagebrush steppe vegetation. *Journal of Arid Environments*, **64**, 670-697.

Brysting AK, Fay MF, Leitch IJ, Aiken SG (2004) One or more species in the arctic grass genus *Dupontia*? - a contribution to the Panarctic Flora project. *Taxon*, **53**, 365-382.

Chapin FS, Shaver GR, Giblin AE, Nadelhoffer KJ, Laundre JA (1995) Responses of arctic tundra to experimental and observed changes in climate. *Ecology*, **76**, 694-711.

Cody WJ (1996) *Flora of the Yukon Territory*. NRC Research Press, Ottawa, 643 pp.

Convey P, Pugh PJA, Jackson C, Murray AW, Ruhland CT, Xiong FS, Day TA (2002) Response of Antarctic terrestrial microarthorpods to long-term climate manipulations. *Ecology*, **83**, 3130-3140.

Dollery R, Hodkinson ID, Jonsdottir IS (2006) Impact of warming and timing of snow melt on soil microarthropod assemblages associated with *Dryas*-dominated plant communities on Svalbard. *Ecography*, **29**, 111-119.

Drake BG, Gonzalez Meler MA, Long SP (1997) More efficient plants: A consequence of rising atmospheric CO_2? *Annual Review of Plant Physiology and Plant Molecular Biology*, **48**, 609-639.

Eskelinen A, Oksanen J (2006) Changes in abundance, composition and species richness of mountain vegetation in relation to summer grazing by reindeer. *Journal of Vegetation Science*, **17**, 245-254.

Flynn DFB, Sudderth EA, Bazzaz FA (2006) Effects of aphid herbivory on biomass and leaf-level physiology of *Solanum dulcamara* under elevated temperature and CO_2. *Environmental and Experimental Botany*, **56**, 10-18.

Fretwell SD (1977) Regulation of plant communities by food-chains exploiting them. *Perspectives in Biology and Medicine*, **20**, 169-185.

Galen C, Stanton ML (1995) Responses of snowbed plant-species to changes in growing-season length. *Ecology*, **76**, 1546-1557.

Gifford EM, Foster AS (1989) Sphenophyta. In: *Morphology and Evolution of Vascular Plants* 3rd edition. 1959 Freeman. New York, 626 pp.

Griffin KL, Anderson OR, Gastrich MD, Lewis JD, Lin GH, Schuster W, Seemann JR, Tissue DT, Turnbull MH, Whitehead D (2001) Plant growth in elevated CO_2 alters mitochondrial number and chloroplast fine structure. *Proceedings of the National Academy of Sciences of the United States of America*, **98**, 2473-2478.

Heegaard E, Vandvik V (2004) Climate change affects the outcome of competitive interactions – an application of principal response curves. *Oecologia* **139**, 459-466.

Hollister RD, Webber PJ, Bay C (2005) Plant response to temperature in Northern Alaska: Implications for predicting vegetation change. *Ecology*, **86**, 1562-1570.

Ims RA, Fuglei E (2005) Trophic interaction cycles in tundra ecosystems and the impact of climate change. *Bioscience*, **55**, 311-322.

IPCC Report (2001) IPCC Third Assessment Report – Climate Change 2001.

Jefferies RL, Rockwell RF, Abraham KE (2004) Agricultural food subsidies, migratory connectivity and large-scale disturbance in arctic coastal systems: A case study. *Integrative and Comparative Biology*, **44**, 130-139.

Karlsson PS, Tenow O, Bylund H, Hoogesteger J, Weih M (2004) Determinants of mountain birch growth in situ: effects of temperature and herbivory. *Ecography*, **27**, 659-667.

Klanderud K (2005) Climate change effects on species interactions in an alpine plant community. *Journal of Ecology*, **93**, 127-137.

Klein JA, Harte J, Zhao XQ (2005) Dynamic and complex microclimate responses to warming and grazing manipulations. *Global Change Biology*, **11**, 1440-1451.

Malanson GP, Cairns DM (1995) Effects of increased cloud cover on a montane forest landscape. *Ecosience*, **2**, 75-82.

Marchand FL, Mertens S, Kockelbergh F, Beyens L, Nijs I (2005) Performance of High Arctic tundra plants improved during but deteriorated after exposure to a simulated extreme temperature event. *Global Change Biology*, **11**, 2078-2089.

McIntire EJB, Hik DS (2002) Grazing history versus current grazing: leaf demography and compensatory growth of three alpine plants in response to a native herbivore (*Ochotona collaris*). *Journal of Ecology*, **90**, 348-359.

McNaughton SJ (1984) Grazing lawns - animals in herds, plant form, and coevolution. *American Naturalist*, **124**, 863-886.

Milchunas DG, Lauenroth WK (1993) Quantitative effects of grazing on vegetation and soils over a global range of environments. *Ecological Monographs*, **63**, 327-366.

Neilson RP, Pitelka LF, Solomon AM, Nathan R, Midgley GF, Fragoso JMV, Lischke H, Thomspon K (2005) Forecasting regional to global plant migration in response to climate change. *BioScience*, **55**, 749-759.

Oksanen L, Fretwell SD, Arruda J, Niemela P (1981) Exploitation ecosystems in gradients of primary productivity. *American Naturalist*, **118**, 240-261.

Olofsson J (2006) Short- and long- term effects of changes in reindeer grazing pressure on tundra heath vegetation. *Journal of Ecology*, **94**, 431-440.

Roy BA, Gusewell S, Harte J (2004) Response of plant pathogens and herbivores to a warming experiment. *Ecology*, **85**, 2570-2581.

Srivastava DS, Jefferies RL (1996) A positive feedback: Herbivory, plant growth, salinity, and the desertification of an Arctic salt-marsh. *Journal of Ecology*, **84**, 31-42.

Stenstrom A, Jonsdottir IS (1997) Responses of the clonal sedge, *Carex bigelowii*, to two seasons of simulated climate change. *Global Change Biology*, **3**, 89-96.

Veteli TO, Kuokkanen K, Julkunen-Tiitto R, Roininen H, Tahvanainen J (2002) Effects of elevated CO_2 and temperature on plant growth and herbivore defensive chemistry. *Global Change Biology*, **8**, 1240-1252.

Visser ME, Both C (2005) Shifts in phenology due to global climate change: the need for a yardstick. *Proceedings of the Royal Society B-Biological Sciences*, **272**, 2561-2569.

Wahren CHA, Walker MD, Bret-Harte MS (2005) Vegetation responses in Alaskan arctic tundra after 8 years of a summer warming and winter snow manipulation experiment. *Global Change Biology*, **11**, 537-552.

Walker MD, Wahren CH, Hollister RD, Henry GHR, Ahlquist LE, Alatalo JM, Bret-Harte MS, Calef MP, Callaghan TV, Carroll AB, Epstein HE, Jonsdottir IS, Klein JA, Magnusson B, Molau U, Oberbauer SF, Rewa SP, Robinson CH, Shaver GR, Suding KN, Thompson CC, Tolvanen A, Totland O, Turner PL, Tweedie CE, Webber PJ, Wookey PA (2006) Plant community responses to experimental warming across the tundra biome. *Proceedings of the National Academy of Sciences of the United States of America*, **103**, 1342-1346.

Zimov SA, Chuprynin VI, Oreshko AP, Chapin FS, Reynolds JF, Chapin MC (1995) Steppe-tundra transition – a herbivore-driven biome shift at the end of the Pleistocene. *American Naturalist*, **146**, 765-794.

Zvereva EL, Kozlov MV (2006) Consequences of simultaneous elevation of carbon dioxide and temperature for plant-herbivore interactions: a metaanalysis. *Global Change Biology*, **12**, 27-41.

APPENDIX A

Difficulties Associated with Precisely Measuring Temperature in OTC and Grazed Treatments

The moss canopy and the trampling effects of geese made temperature comparisons among treatments difficult. Geese changed the structure of the vegetation by compacting the moss layer to the same level as the saturated soils, this provided a clear boundary between the ground and air. This clear ground-air boundary was absent in ungrazed plots. Intact moss continuously grew on top of dead moss and created a canopy that was predominantly above the water level. Thus the surface was a clear boundary in the grazed plots, and a 2-10 cm band of moss canopy in the ungrazed plots. There was a strong thermal gradient between 15 cm below the surface and 5 cm above the surface. Thus temperature comparisons between treatments are dependent on accurately placing temperature loggers at equivalent depths and heights, a task compounded with the difficulty associated with determining the surface.

I used iButtons to record temperatures on plots. Due to limited numbers of iButtons I measured the thermal gradients comparing the ungrazed × ambient plots with the ungrazed × OTC plots (2 replicates), the 5hr grazed × ambient plots with the ungrazed × ambient plots (5 replicates), and the 5hr grazed × ambient plots with the 5hr grazed × OTC plots (5 replicates). I also measured the surface temperature over a 20 day period in July (Tables 1 and 2), however it is likely that dataloggers were not uniformly placed at the 'surface'. Additionally, the functioning of the OTC may change over the course of the growing season. Both replicates from ungrazed plots are presented (Figure A-1 and Figure A-2). OTCs increased maximum daily temperatures, however in one of the OTCs a cooling effect was observed at 10 and 15 cm below the surface. A representative plot from

the 5hr grazed OTC and 5 hr grazed ambient combination (Figure A-3) demonstrates warming of the soil down to 10 cm below the surface. A representative plot from the 5 hr grazed × ambient and ungrazed × ambient combination is also presented (Figure A-4). Herbivory tended to increase the variability in surface temperature.

Table A-1: ANOVA table of surface maximum, minimum, and mean temperatures over a 20 day period in July.

	Max		Min		Mean	
	$F_{(Numdf,Dendf)}$	P	$F_{(Numdf,Dendf)}$	P	$F_{(Numdf,Dendf)}$	P
Temperature	$0.44_{(1,84.4)}$	0.5068	$0.85_{(1,63.3)}$	0.3588	$0.06_{(1,48.7)}$	0.8030
Graze	$15.27_{(2,84.4)}$	<0.0001	$0.82_{(2,63.3)}$	0.4469	$6.19_{(2,48.7)}$	0.0004
Temperature × Graze	$0.82_{(2,84.4)}$	0.4449	$4.84_{(2,63.3)}$	0.0110	$2.87_{(2,48.7)}$	0.0663

Table A-2: Mean minimum, mean and maximum temperatures over a 20 day period in July.

Treatment	Minimum	Mean	Maximum
0 hrs Ambient	5.1 °C	7.6 °C	10.6 °C
0 hrs OTC	5.3 °C	7.5 °C	10.6 °C
1 hr Ambient	5.1 °C	7.3 °C	10.2 °C
1 hr OTC	4.9 °C	7.0 °C	9.7 °C
5 hrs Ambient	4.8 °C	6.7 °C	9.0 °C
5 hrs OTC	5.4 °C	7.0 °C	9.2 °C

Figure A-1: Differences in temperature between ungrazed × OTC and ungrazed × ambient combinations from 14:00 8 July 2005 to 19:00 10 July 2005. Temperatures recorded every three minutes. OTCs increased maximum daily temperatures over this time period. A cooling effect was not observed in this plot at 15 cm below the surface.

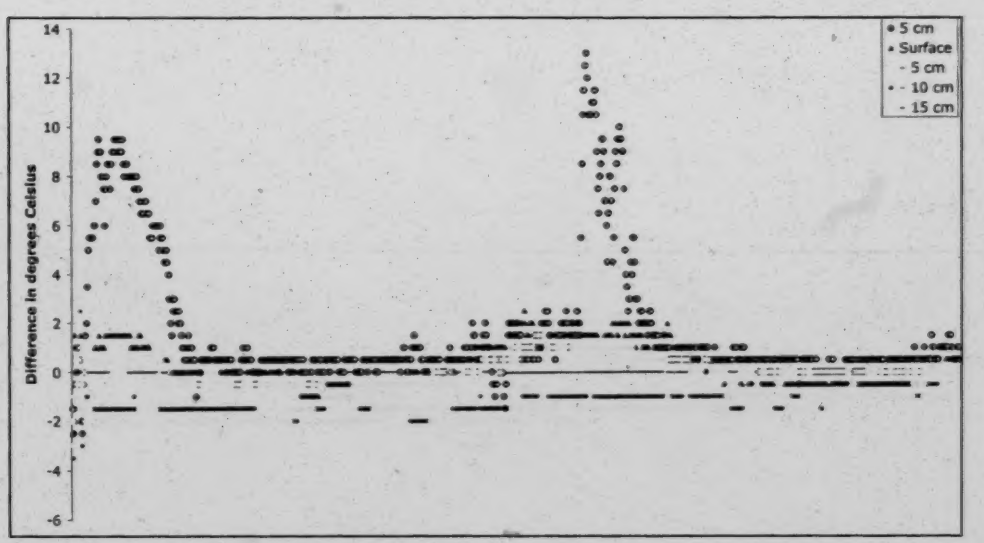

Figure A-2: Differences in temperature between ungrazed × OTC and ungrazed × ambient combinations from 14:00 8 July 2005 to 19:00 10 July 2005. Temperatures recorded every three minutes. OTCs increased maximum daily temperatures over this time period. A cooling effect was observed in this plot at 10 and 15 cm below the surface.

Figure A-3: Differences in temperature between 5 hr grazed × OTC and 5 hr grazed × ambient plot from 20:00 31 July 2005 to 22:00 7 August 2005. Temperatures recorded every five minutes. OTCs increased temperatures down to 10 cm below the surface over this time period.

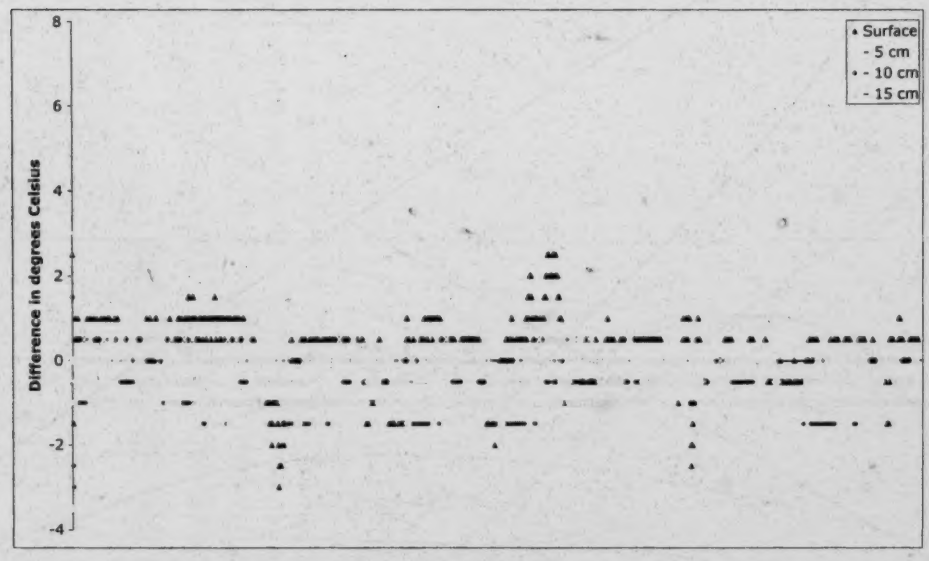

Figure A-4: Differences in temperature between 5 hrs grazed × ambient and ungrazed ambient from 9:00 14 August 2005 to 21:30 22 August 2005. Temperatures were recorded every six minutes. Herbivory tended to increase the variability in surface temperature.